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Precipitation Chemistry and Chemical Limnology of Fertilized and Natural Lakes at Saqvaqjuac, N.W.T.

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Welch, H. E., and J. A. Legault. 1986. Precipitation chemistry and chemical limnology of fertilized and natural lakes at Saqvaqjuac, N.W.T. Can. J. Fish. Aquat. Sci. 43: 1104–1134.

Precipitation at Saqvaqjuac (northwest coast of Hudson Bay, 60°39′N) had high concentrations of sea salts, was moderately acidic, and had less SO_4 and total N than lower latitude precipitation, although SO_4 sources were distant. Watershed retention was high for H^+, but negative for other elements as a consequence of isostatic rebound. Annual element runoff was a function of the timing of melt runoff and summer rain events because of permafrost. Lake retention of Si was higher than P because of the different times of loading, late summer versus spring. Conservative element mass did not change overwinter except in low-elevation Spring Lake, where residual Cl, Na, and K diffused from the sediments. Phosphorus and N were the only elements incorporated into black ice. As a result of freezeout and incomplete meltwater mixing beneath lake ice, element concentrations were 1.6 times higher in lakes than inflows, and major ion turnover times were 1.5–2.0 times higher than water turnover times.

À Saqvaqjuac, sur la côte nord-ouest de la baie d'Hudson, à 60°39′N, les précipitations contiennent de fortes concentrations de sels marins, sont modérément acides et contiennent moins de SO_4 et d'azote total que les précipitations sous des latitudes plus basses, les sources de SO_4 étant éloignées. Le bassin hydrographique a une forte rétention de H^+, mais enregistre une perte des autres éléments due au relèvement isostatique. Le lessivage annuel des éléments est fonction de la date du dégel et des pluies d'été, en raison du pergélisol. La rétention de Si dans les lacs est plus élevée que celle de P en raison des différentes périodes de chargement, c'est-à-dire à la fin de l'été et au printemps. La masse des éléments dissous ne change pas durant l'hiver, sauf au lac Spring, situé à faible altitude, où le Cl, le Na et le K résiduels proviennent des sédiments. Le P et le N sont les seuls éléments contenus dans la glace noire. En raison du dégel et du mélange incomplet des eaux de fonte sous la glace des lacs, on a observé des concentrations d'éléments 1,6 fois plus importantes dans les lacs que dans les eaux d'entrée, et la fréquence de renouvellement des principaux ions est de 1,5 à 2 fois supérieure à celle de l'eau.

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This paper is one of a series dealing with limnological investigations at Saqvaqjuac, a Department of Fisheries and Oceans research site on the northwest coast of Hudson Bay (63°39′N, 90°39′W) 36 km north of the hamlet of Chesterfield Inlet. The major thrust of the project was a whole-lake phosphorus and nitrogen addition experiment to quantify the response of arctic lakes to nutrient addition. During the investigation, we studied meteorology, hydrology, chemical, physical, and biological limnology, and fish populations. Background information on the site can be found in Welch (1985).

Here we discuss results of our investigations into the chemistry of Saqvaqjuac lakes, beginning with precipitation chemistry, and then element runoff from the land, mass balance in the lakes, and finally retention and loss from the lakes. Although there have been a number of hydrological studies on permafrost watersheds, this is the first detailed investigation of element input/output on continuous permafrost watersheds of which we are aware. The data were gathered primarily to investigate the nutrient metabolism of natural and artificially fertilized lakes, but they also apply to the larger geochemical picture. Thus we expected to find differences in the amount and timing of element flux through permafrost drainages because there is no groundwater percolation and the rock surface available for weathering is thereby decreased. We also expected to find differences in seasonal lake chemistry as a result of sharply seasonal inputs and prolonged ice cover.

The geochemical cycle as it affects Saqvaqjuac lakes is diagrammed in Fig. 1. The primary source for most elements is rock and soil weathering and subsequent loss from the land as particulate and solute runoff. There may also be washout of sea salts residual from glacial rebound. Element input via precipitation constitutes an important component of solute output from a watershed. Such atmospheric input may result from natural processes, as for nitrate or sea salts, or from long-range transport of anthropogenic pollutants, as for sulfate. Lakes also receive atmospheric inputs directly as well as via runoff. Element concentrations in lakes are changed by freezeout (cryoconcentration), dilution by meltwater, and exchange with sediment, where retention occurs. Some amount leaves the lake

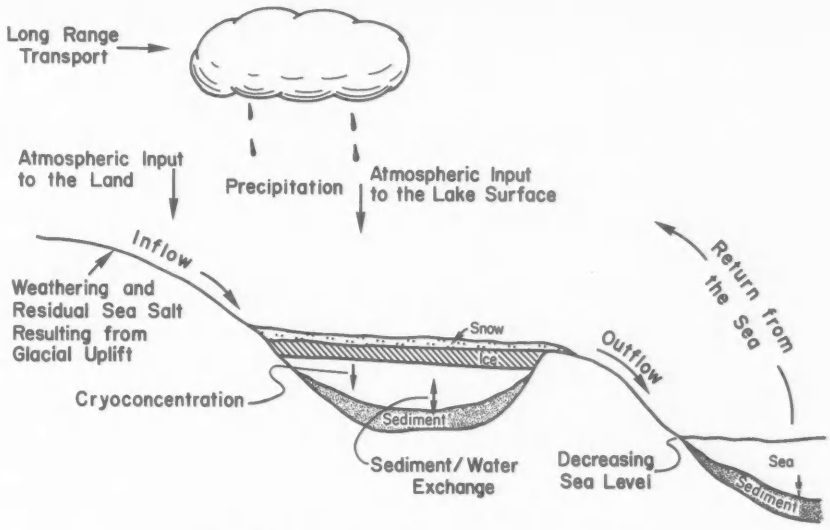

FIG. 1. Geochemical cycle as it affects Saqvaqjuac lakes.

TABLE 1. Morphometry of Saqvaqjuac lakes discussed in this paper.

Lake	Z_{mean}	Z_{max}	A_0 (ha)[a]	A_D (ha)[b]	$A_D:A_0$	% ice volume[c]	Elevation (m above msl)[d]
Jade	1.82	5.2	3.63	27.9	7.7	77	31
Far	3.61	8.9	3.70	16.6	4.5	46	18
P & N	3.28	10.2	7.09	28.6	4.0	47	16
Spring	2.71	7.1	6.93	30.6	4.4	56	3

[a]Lake area.
[b]Drainage area excluding lake area.
[c]At 2 m ice thickness.
[d]Far and P & N lakes accurately surveyed; Spring Lake approx. ±1 m; Jade Lake ±5 m.

via the outflow, to accumulate in marine sediments.

Methods

Description of Study Area

Saqvaqjuac bedrock is Precambrian granitic gneiss scoured by glaciation which left ridge tops and steeper slopes nearly till-free, and lower slopes and valleys with a shallow overburden of coarse glacial till, reworked by marine inundation below about 160 m asl (Andrews 1969). The till is of the same granitic composition as the bedrock although calcareous fragments up to a few kilograms in size occur as scattered erratics. Clam shells are also abundant at lower elevations. Relief is typically a few tens of metres, with numerous broken ridges and valleys that are a few hundreds of metres in width and 1 to several kilometres in length. The area is underlain by about 300 m of permafrost, with an active zone about 1 m maximum depth (Dalton 1981). Vegetation is typically moss and lichens in shallow depressions on exposed bedrock, and continuous heath tundra in well-drained soil-covered sites, with wet sedge/cotton grass meadows in low, wet sites.

Lakes are numerous, comprising 17% of the land surface, and occupy ice-scour depressions in bedrock, although outlets are largely till-controlled. Experimental lakes are small (3.6–6.9 ha), single basin headwater lakes 5–10 m maximum depth (Table 1), ranging from ≈3 m asl (Spring Lake) to ≈31 m asl (Jade Lake). Water is typically low in solutes (conductance 40–100 $\mu S \cdot cm^{-1}$; total dissolved solids 15–45 $mg \cdot L^{-1}$). Annual precipitation is 29 cm, about half falling as rain during June–September. The annual spring snowmelt begins about 1 June and lasts a month, so runoff is precipitous early in the summer and decreases rapidly. The Saqvaqjuac River watershed (607 km^2) also contains numerous lakes, and the water course itself is composed almost entirely of a lake chain connected by short stretches of rapids. As a result, its annual hydrological regime and solute discharge are highly modified compared with entirely terrestrial watersheds in the area. Its headwaters reach elevations above the level of the most recent marine inundation.

In addition to the experimental lakes, we maintained an entirely terrestrial research watershed, the "Meadow," 15.4 ha of typical rock outcrop and tilled valley, with a permanent weir where continuous discharge was measured and chemical samples taken, and with precipitation gauges on the watershed (see Dalton 1981 for details). This controlled watershed gave us our best data on inputs and outputs on the land surface.

Fertilization

In July–August of 1979–83, phosphorus (P) alone was added to Far Lake, and P and nitrogen (N) were added to

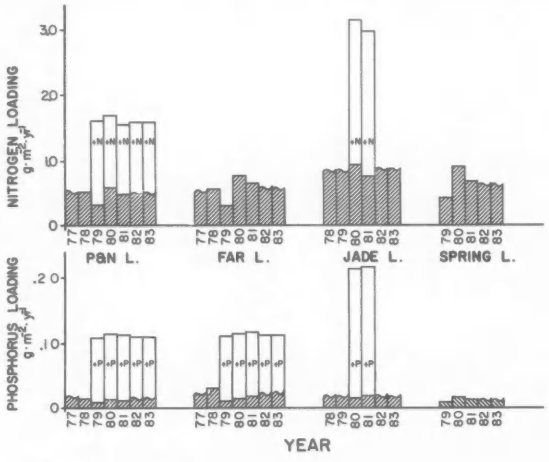

FIG. 2. Natural and artificial P and N supply per square metre of lake surface for research lakes. Shaded areas are natural loading. ~ signifies natural (unmeasured) loading only. Nominal artificial loading levels were 0.1 g $P \cdot m^{-2} \cdot yr^{-1}$ in P & N and Far lakes, 1.0 g $N \cdot m^{-2} \cdot yr^{-1}$ in P & N Lake, and 0.2 g P and 2.0 g $N \cdot m^{-2} \cdot yr^{-1}$ in Jade Lake. Spring Lake received no additional nutrients.

P & N Lake. Jade Lake received P and N in 1979 and 1980. Spring Lake was studied 1978–81 as a control. Fertilizer loading rates are summarized in Fig. 2.

Phosphorus as H_3PO_4 was diluted >100:1 with lake water and added twice weekly for 10 wks, starting at ice-out, by draining the nutrient solution through the drain plug of a boat into the prop wash as the boat moved about the lake. Nitrogen as $NaNO_3$ was diluted about 10:1 and added simultaneously with the P.

Chemistry

Data were collected May–September of 1977–81, for two winters (1977–78 and 1980–81), and small amounts of chemical data were collected in 1983. Background data were collected in the prefertilization years of 1977 and 1978 in P & N and Far lakes, but no prefertilization data was collected from Jade Lake. The summer 1977 data is reported in de March and Rudy (1978).

Water samples were collected with a Van Dorn water sampler from the lakes every week during the ice-off period and every second week during the ice-on period. Samples during the ice-off period were taken only at the surface and near the bottom, because detailed sampling showed no chemical stratification, even during temporary thermal stratification. During the ice-on period when the lakes were chemically stratified, samples were taken through a hole in the ice, starting just below the depth of the ice to the bottom, at 2-m intervals. The samples were returned to the laboratory in opaque plastic bottles. Analysis for dissolved inorganic and organic carbon (DIC, DOC), soluble reactive silica (Si), total phosphorus (TP), total dissolved nitrogen (TDN), chlorophyll *a* (Chl), conductivity, and pH were conducted at the Saqvaqjuac laboratory the same day as collected. Hydrogen ion was calculated from pH. Subsamples were sent to the Freshwater Institute for analysis of particulate carbon, nitrogen, and phosphorus (PC, PN, PP) and dissolved chloride (Cl), sulphate (SO_4), calcium (Ca), magnesium (Mg), potassium (K), sodium (Na), iron (Fe), and manganese (Mn). Iron and Mn were usually below detectable levels (<0.04 and <0.01 $mg \cdot L^{-1}$, respectively) in 1977 (de March and Rudy 1978), and were not determined after 1977. All methods for analyses were according to Stainton et al. (1977) except for Chl, which was extracted from glass fiber filters by sealing the filter in glass vials containing 10 mL of 90% acetone for 24 h. The vial was then shaken, the solution decanted directly into a fluorometer curvette, and the fluorescence measured. The fluorometer was calibrated against lettuce chlorophyll according to Stainton et al. (1977). Acid ratios were not measured. Dissolved ions are symbolized without the charge sign, e.g. H equals H^+.

Calculation of Element Fluxes

Summer precipitation, taken as total rain and snowfall 1 May – 30 September, is from Dalton (1981) and R. Newbury (Freshwater Institute, Winnipeg, Man., pers. comm.), supplemented with precipitation data for Chesterfield Inlet (Canada Department of the Environment records) early and late in the season if Saqvaqjuac was unoccupied. Chemical analyses were performed on bulk[1] precipitation samples collected 1 m above ground in an open 1-m^2 acrylic collector which drained into a covered 20-L polyethylene carboy. Aside from an occasional insect, there was little visible particulate contamination. Dryfall was usually automatically included because rain events were frequent, although several times the collector was rinsed after a long period (10 d) without rain. Typically, about half of each summer's precipitation was analyzed (Table 2).

Summer chemical input via precipitation was calculated as follows. For each event that was analyzed chemically, concentration was multiplied by the volume of the event as measured with a standard rain gauge (Dalton 1981) and the inputs summed and divided by the total volume of the events to obtain the mean concentration of each element in summer precipitation. This was then multiplied by the total summer precipitation to obtain total input by precipitation.

Winter precipitation was from Canada Department of the Environment meteorological records at Chesterfield Inlet. Trace events were presumed to be 0.1 mm. Chemical concentrations were determined on nine fresh, undrifted snowfalls collected in 1978, 1980, and 1981, skimmed with a clean acrylic plastic sheet from the clear ice surface of nearby lakes, and melted in clean polyethylene bags. Distilled deionized water placed in identical bags served as controls. The mean concentration of each element was multiplied by the total snowfall (1 October – 30 April) for each year. The elemental input added directly to a lake by accumulated snow melting on the lake's surface was calculated from mean snow depth in early May as determined from surveys on each lake, multiplied by the chemical concentrations in fresh snow. Although the windblown snowpack on the lake surfaces probably had higher element concentrations than fresh snow, any difference is negligible to our results because the contribution by melting snow on the experimental lakes' surfaces was at most a few percent of total supply for all dissolved elements except H.

Element inputs to the lakes from their surrounding watersheds were calculated as follows. Concentrations were determined weekly on all surface inflows during the runoff period, typically four to six inflows on each lake during peak runoff, decreasing in midsummer as some inflows dried up. Two

[1]Wetfall plus an unknown part of dry fall.

inflows (from Upper Spring Lake into Spring Lake, and from "Art's Pond" into Far Lake) drained a larger area than the rest, and when concentrations were much different in them, their contribution was calculated separately from the other inflows. Otherwise, mean element concentration in all inflows for a given lake were plotted against time, concentration curves drawn by eye, and interpolated concentrations from the graphs multiplied by measured runoff on a daily basis to obtain inputs from the watersheds.

Only the dissolved fractions of most elements were considered. Only P and N had both dissolved and particulate forms measured, and for those two elements, in runoff, the particulate form was a small fraction of each.

Element mass balances in the lakes was calculated as follows. For ice-free conditions, the concentration at the midpoint of each metre depth was computed by linear interpolation or extrapolation from the two known concentrations, multiplied by the lake volume at each metre interval, summed, and divided by the lake surface area. For ice-on conditions the same procedure was used for the unfrozen water column except that concentrations and volumes were calculated for 5-cm depth intervals for the 0–2 m depth zone to account for the volume of ice (see Welch and Bergmann 1985a for details). The chemical content of the lake ice was also taken into account when calculating winter mass balances. Element concentrations in lake ice were determined on large (≥30 cm diameter), unbroken columns of ice removed from each lake. Each column was sectioned transversely at 20-cm intervals and the outside surface of each resultant block shaved off with a clean steel chisel to a depth of ≥5 mm. Only clean unfractured blocks were used. Each block was melted in covered glass containers. Distilled deionized water held in similar containers served as controls.

Results and Discussion

Input by Precipitation

Mean annual precipitation from 1932 to 1981 at Chesterfield Inlet was 291 mm (not shown), and the mean annual precipitation at Saqvaqjuac was 290 mm, using Chesterfield Inlet snowfall and five summers of Saqvaqjuac rainfall (see Table 4). Precipitation was lowest in midwinter, increased sharply in May–June, and peaked in July–August (Fig. 3), which corresponds closely with the annual temperature cycle (Welch 1985) and the open water season. About 64% of the annual precipitation at Saqvaqjuac fell in the 5-mo period of 1 May – 31 September (see Table 4).

Element concentrations in rainfall were extremely variable, with 95% confidence limits ranging up to 10 times the mean for some compounds (Table 2). Concentrations varied less in fresh snowfall (Table 3). Hydrogen, SO_4, and TN concentrations were approximately the same in snow and rain, K concentrations were usually below the detectable limit of 0.02 $mg \cdot L^{-1}$, and Cl, Mg, Ca, Na and TP were more concentrated in rain than in snow. About one third of total precipitation occurred during the winter 7 mo, with winter inputs of Cl, Na, Mg, Ca, and TP proportionately even lower (Table 4).

Hydrogen ion input via precipitation was high, 17–32 $g \cdot ha^{-1}$ annually (Table 4). The mean pH of fresh snow was 4.65 (Table 3), and that of summer rainfall was 4.80 (Table 2).

Phosphorus concentrations were extremely low but detectable in snow (1.4 $\mu g \cdot L^{-1}$), and were much higher, about 8 $\mu g \cdot L^{-1}$, in rainfall, so over 80% of the P input by precipitation occurred in summer. Nitrogen concentrations were much higher than P, 318 $\mu g \cdot L^{-1}$ in winter and 292 $\mu g \cdot L^{-1}$ in summer. On average, about half the total N (TN) input via precipitation occurred in winter.

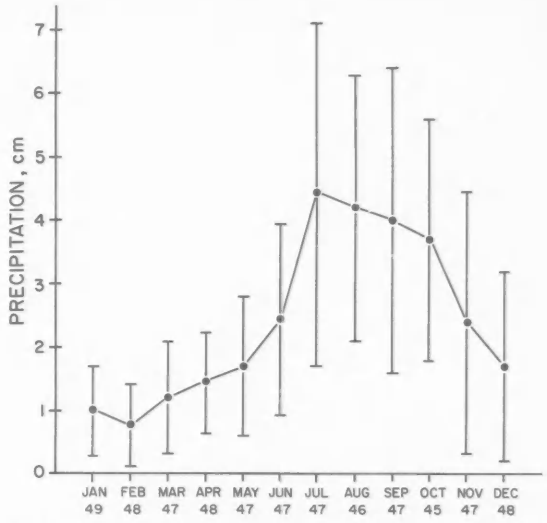

FIG. 3. Mean monthly precipitation recorded at Chesterfield Inlet (Department of Transport and Department of the Environment meteorological records, 1932–81). Numbers below abscissa are numbers of years with data. One standard deviation shown. Trace events assigned a value of 0.1 mm.

When total cations and anions in precipitation are compared, the data are again variable on a year-to-year basis (Table 4). The overall volume-weighted mean for four summers' rainfall was 69.5 milliequivalents (mEq) cations $\cdot m^{-3}$ and 51.8 mEq anions $\cdot m^{-3}$, a cation to anion ratio of 1.34. Concentration in snow was even more strongly skewed, with 44.3 mEq cations $\cdot m^{-3}$ and 27.1 mEq anions $\cdot m^{-3}$ (Table 3), a cation to anion ratio of 1.63. The inclusion of detectable limits when calculating means (see Table 4) cannot account for the discrepancy, since the major ion affected was SO_4, and "true" concentrations would decrease the sum of negative ions even further. Charge balances calculated for Saqvaqjuac lake waters averaged close to 1.0 (see Table 20), indicating that analytical procedures were not biased. However, many determinations on precipitation were close to the limits of detection and a systematic error may well have been present. Scheider et al. (1979) noted the same problem for their analyses of precipitation and lake water in south-central Ontario.

Total input by summer precipitation was not correlated with total rainfall for any element (Table 4). Although 1980 tended to have higher solute inputs and 1978 lower solute inputs, 1977, 1979, and 1981 data showed no trends. This was typified by Na, which had high input in 1981 and low input in 1979, at essentially the same rainfall. Sulfate input in 1978 was even higher than in 1980, despite the much higher rainfall in 1980.

We calculated the relative contribution of sea salt to Saqvaqjuac precipitation by assuming that all Cl in precipitation originated from sea salt (Junge and Werby 1958) and calculating the associated amounts of Mg, Ca, Na, and SO_4 using sea salt ratios from Connors and Kester (1974) (K concentrations were too low to analyze further). The results showed that for the overall mean of four summers and three

TABLE 2. Mean ionic concentrations[a] and conductance in summer precipitation at Saqvaqjuac.

Year	Mean pH[b]	Concn.	±95%	mEq·m^{-3}	% precip. vol. analyzed	% of analyzed vol. < det. limit[c]
			H (concn. μg·L)			
1977	4.57	26.9	72.1	26.9	83	0
1978	5.25	5.6	28.2	5.6	55	0
1979	4.89	12.9	78.1	—	64	0
1980	5.07	8.6	11.9	8.6	51	0
1981	4.50	25.2	64.2	25.2	38	0
			SO_4 (concn. mg·L^{-1}; detectable limit 0.2 mg·L^{-1})			
1977	—	<0.57	3.32	<11.9	70	39
1978	—	<0.98	9.59	<20.4	68	38
1979	—	—	—	—	—	—
1980	—	<0.44	3.09	<9.2	38	22
1981	—	1.54	8.76	32.0	36	0
			Cl (concn. mg·L^{-1}; detectable limit 0.2 mg·L^{-1})			
1977	—	2.03	10.03	57.2	64	0
1978	—	1.27	16.86	35.8	54	0
1979	—	—	—	—	—	—
1980	—	0.98	9.70	27.6	38	0
1981	—	1.02	5.60	28.7	36	0
			K (concn. mg·L^{-1}; detectable limit 0.02 mg·L^{-1})			
1977	—	<0.10	0.66	<2.6	71	37
1978	—	<0.02	—	<0.5	59	100
1979	—	<0.04	0.18	—	20	69
1980	—	<0.02	0.10	<2.0	29	89
1981	—	<0.08	0.27	<0.5	36	7
			Mg (concn. mg·L^{-1}; detectable limit 0.01 mg·L^{-1})			
1977	—	<0.14	0.99	<11.5	73	57
1978	—	0.06	0.31	4.9	48	0
1979	—	0.12	0.30	—	16	0
1980	—	0.09	0.55	7.4	49	0
1981	—	0.10	0.23	8.2	29	0
			Ca (concn. mg·L^{-1}; detectable limit 0.05 mg·L^{-1})			
1977	—	<0.18	0.67	<9.0	55	50
1978	—	0.17	0.39	8.5	43	0
1979	—	0.31	0.81	—	16	0
1980	—	<0.20	1.76	5.0	30	23
1981	—	0.29	0.54	14.5	29	0
			Na (concn. mg·L^{-1}; detectable limit 0.01 mg·L^{-1})			
1977	—	1.63	8.47	70.9	63	0
1978	—	0.35	2.57	15.2	48	0
1979	—	0.49	2.83	—	20	0
1980	—	0.45	4.64	19.6	31	0
1981	—	1.82	12.60	79.1	36	0
			NO_3 (concn. μg·L^{-1}; detectable limit 1.0 μg·L^{-1})			
1977	—	32.6	100.4	1.1	47	0
1978	—	21.1	132.7	0.7	40	0
			NH_3 (concn. μg·L^{-1}; detectable limit 1.0 μg·L^{-1})			
1977	—	55.5	203.7	3.1	77	0
1978	—	14.6	134.5	0.8	50	0
			TN (concn. μg·L^{-1}; detectable limit 20 μg·L^{-1})			
1977	—	361	963	—	75	0
1978	—	264	1027	—	64	0
1979	—	228	707	—	62	0
1980	—	204	887	—	63	0
1981	—	403	1190	—	28	0

TABLE 2. (*Concluded*)

Year	Mean pH[b]	Concn.	±95%	mEq·m^{-3}	% precip. vol. analyzed	% of analyzed vol. < det. limit[c]
			TP (concn. μg·L^{-1}; detectable limit 1.0 μg·L^{-1})			
1977	—	5.9	19.4	—	81	0
1978	—	3.4	29.4	—	54	0
1979	—	6.4	16.9	—	56	0
1980	—	4.8	25.5	—	62	0
1981	—	15.8	69.1	—	34	0
			Conductance (μS·cm^{-1})			
1977	—	16.7	40.4	—	81	0
1978	—	5.4	13.6	—	58	0
1979	—	11.6	27.1	—	57	0
1980	—	7.0	32.6	—	44	0
1981	—	17.7	57.5	—	37	0

	1977	1978	1980[d]	1981[d]
Σ Anions	<70.2	<56.9	<36.8	60.7
Σ Cations	<124.0	<35.5	<41.1	<129.0

Mean volume-weighted concentration in summer rainfall, anions: 51.8
Mean volume-weighted concentration in summer rainfall, cations: 69.5
Overall ratio, cations:anions = 1.34

[a]Volume-weighted, where mean concentration = Σ (concn.) (precip. vol.)/Σ precip. vol.
[b]Mean H corrected to pH.
[c]Where concentrations were below detectable limits, the limit is used to calculate the mean. The reader may interpret the mean concentrations as wished.
[d]No NO_3 or NH_4 data for these years; the two ions are assumed to approximately balance each other.

TABLE 3. Mean element concentrations in fresh snow at Saqvaqjuac from eight snow falls in February 1978, March, May and November 1980, and May 1981.

	mg·L^{-1}						μg·L^{-1}				
	SO_4	Cl	K	Mg	Ca	Na	TP	TN	H	pH	Conductance (μS·cm^{-1})
Mean	<0.66[a]	0.44	<0.02	0.038	0.136	0.27	1.41	318	22.2	4.65	8.47
±95% confidence limits	1.91	0.81	—	0.064	0.353	0.56	7.4	527	64.1	—	10.55
mEq·m^{-3}	<13.7	12.4	<0.05	3.1	6.8	11.7	—	—	22.2	—	—
N	7	6	—	5	5	5	5	5	7	7	8

Σ Anions: <27.1
Σ Cations: <46.0
Cation:anion in fresh snow: 1.70

[a]Includes one measurement below the detectable limit of 0.02 mg·L^{-1}; 0.02 used to calculate mean.

winters of precipitation, Na and Mg inputs were close to those expected from Cl (Table 5), indicating an entirely marine source for those two elements. Only about 20% of summer SO_4 and 12% of summer Ca originated from sea salt, and less than 10% of both elements came from the sea in winter. This is consistent with a nonmarine source for these two compounds, since arctic seas are frozen in winter and therefore contribute less salt than in summer, raising the actual to expected ratio in winter.

Further indications of source for elements in precipitation come from time trends. A plot of Na:Cl in precipitation (Fig. 4) showed no trend, as expected if they had a common source. The SO_4:Cl ratio tended to decrease in late summer (Fig. 4). This was consistent with a distant, nonmarine source for SO_4 because the nearby sea is frozen until July, and Cl concentrations in precipitation should have increased during the open-sea period.

Concentrations of dissolved ions in precipitation at Saqvaqjuac were about as expected based upon temperate North American studies. Solutes derived from the sea (Na, Cl) were much higher than at inland sites in Minnesota, Ontario, and New Hampshire (Table 6) but were not as high as at exposed coastal sites (Junge and Werby 1958) or Char Lake (Table 6). Calcium and Mg were above average. The concentration of TN was lower and the concentrations of TP very much lower than at the other sites in Table 6. Comparing Saqvaqjuac with the limited data from Char Lake, Resolute, N.W.T. (74°42′N), we note that TN, TP, and SO_4 concen-

TABLE 4. Total element input ($g \cdot ha^{-1}$) by precipitation at Saqvaqjuac. The precipitation year is 1 October through the following September.

Element	1977 Summer[a]	1977–78 Winter	1977–78 Summer	1977–78 Total	1979–80 Winter	1979–80 Summer	1979–80 Total	1979–80 Winter	1979–80 Summer	1979–80 Total	1980–81 Winter[b]	1980–81 Summer	1980–81 Total	Mean annual input	Mean percent winter[c]
H	34.7	35.7	9.46	45.2	22.6	14.8	37.4	21.3	24.4	45.7	26.6	28.7	55.3	45.9	62
SO_4	735	<1063	<1656	<2719	<673	—	—	<634	<1250	<1884	<792	1756	<2548	<2384	37
Cl	2619	708	2146	2854	449	—	—	422	2783	3205	528	1163	1691	2583	19
K	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Mg	<182	61	101	162	39	138	177	36	256	292	46	114	160	198	22
Ca	<232	219	287	506	139	356	495	131	<568	<699	163	331	494	<549	29
Na	2103	435	591	1026	275	564	839	259	1278	1537	324	2075	2399	1450	28
TP	7.6	2.3	5.7	8.0	1.4	7.4	8.8	1.4	13.6	15.0	1.7	18.0	19.7	12.9	16
TN	466	512	446	958	324	262	586	305	579	884	382	459	841	817	47
Precip. (mm)	129	161	169	330	102	115	217	96	284	380	120	114	234	290	36

[a] 1 May – 30 September.
[b] Assumes 120 mm winter precipitation (the mean of the three previous winters).
[c] Based on total input for 3 yr, 1977–80.

FIG. 4. Na:Cl and SO_4:Cl ratios (weight:weight) in precipitation at Saqvaqjuac. Arrows indicate points for which Na or SO_4 was below detectable limits, where the limit was used to calculate the ratios.

trations were all higher at Char Lake, along with pH, Ca, and Mg concentrations as well, to be expected, since the Char Lake drainage basin is composed of dolomitic limestone (Rigler 1970).

The mean SO_4 concentrations of 0.88 $mg \cdot L^{-1}$ in summer precipitation was as low as has been found anywhere in the continental United States and Canada except for the west coast (Junge and Werby 1958; Barrie and Hales 1985). The annual SO_4 input of ≈ 2 $kg \cdot ha^{-1}$ (Table 6) was well below the 14–16 $kg \cdot ha^{-1}$ threshold calculated by Gorham et al. (1984) to cause acid damage to aquatic ecosystems. The pH was not as low as over east-central North America (Table 6; Cogbill and Likens 1974; Barrie and Hales 1985), but it was probably slightly lower than in preindustrial times (see Charlson and Rodhe 1982). Recent studies have shown that atmospheric aerosols containing SO_4 and heavy metals are transported into the arctic periodically (Barrie et al. 1981; Rahn 1984; Rahn and McCaffrey 1980). These events are episodic, are associated with increased atmospheric turbidity ("Arctic haze"), and originate from European, Asian, or North American industrial sources. Barrie et al. (1981) predicted a snow pH of 5–5.2 for February–April at Mould Bay in the western high arctic, based upon atmospheric SO_4 concentrations. Here we note that the volume-weighted pH of freshly falled snow that had not been drifted averaged 4.65 at Saqvaqjuac (Table 3), and the mean pH for 5 yr of summer rainfall was 4.80 (from Table 2). That the "acid problem" reaches the high arctic was shown by Koerner and Fisher (1982), who reported increased acidity in permanent ice fields on northern Ellesmere (81°N) during the past 25 yr.

TABLE 5. Factors of enrichment over expected sea salt inputs in precipitation at Saqvaqjuac. Numbers equal the actual weight of a chemical input divided by the expected weight of that chemical's input calculated from Cl inputs and sea salt ratios, assuming that all Cl derives from the sea[a] (1.0 means the actual input equalled the expected; 2.0 means the actual was twice that expected, etc.).

Chemical	Summer 1977	Summer 1978	Summer 1980	Summer 1981	Mean summer[b]	Mean winter[c]	Mean annual precipitation[d]
SO_4	<2.0	<5.5	<3.2	10.8	<4.4	<10.7	<5.7
Mg	<1.0	0.7	1.4	1.5	<1.1	1.3	<1.1
Ca	<4.2	6.3	<9.6	13.4	7.6	14.5	<9.0
Na	1.4	0.5	0.8	3.2	1.2	1.1	1.2

[a] Ratio of elements in sea water from Connors and Kester (1974).
[b] Based on total input, not mean of ratios, four summers.
[c] Based on total input, not mean of ratios, three winters (Table 4).
[d] Four summers and three winters.

TABLE 6. Volume-weighted mean element concentration ($mg \cdot L^{-1}$) in precipitation for selected areas of North America.

Location	Years	Conductance ($\mu S \cdot cm^{-1}$)	pH	Ca	Mg	Na	Cl	SO_4	TN	TP	Source
Char Lake, Resolute, N.W.T.[a]	1971	—	7.1	4.19	0.66	0.88	4.85	2.0	0.43	0.035	Schindler et al. 1974
Saqvaqjuac, N.W.T.	1977–81	8.9	4.80	0.19	0.07	0.50	0.89	0.82	0.28	0.004	This study
ELA, northwestern Ontario	1970–82	14.2	4.92	0.48	0.11	0.20	0.45	1.61	0.81	0.033	G. A. Linsey, Freshwater Institute, Winnipeg, Man., pers. comm.
Marcell Experimental Forest, northcentral Minnesota	1978–80	11.3	4.30	0.30	0.05	0.35	0.17	1.73	1.41 (NO_3 only)	0.007 (PO_4 only)	Verry 1983
HBEF, northern New Hampshire	1963–74	—	4.14	0.16	0.04	0.12	0.47	2.9	1.47 (NO_3 only)	0.008 (PO_4 only)	Likens et al. 1977; Table 4

[a] Average of mean snow and mean rain values.

We too have noted occasional hazy conditions in February–March at Saqvaqjuac and have observed black scums collecting on meltwater pools on the sea ice in June, on the northwest coast of Hudson Bay, and also at Barrow Strait (74°N). Microscopically the scums from the Saqvaqjuac area appear to be uniformly composed of amorphous gray–black soot particles. The downwind edges of melt pools where the scum collects have a lower albedo and appear to melt more quickly than other parts of the pools. We therefore wonder if the long-range transport of industrially derived aerosols to the arctic might have an effect on the albedo of snow cover, as well as an effect on water chemistry.

The input of elements via precipitation is a function of meteorological conditions and air mass histories, resulting in differences between days, months, and even years. Barrie et al. (1981) back-calculated air mass trajectories and found that major episodic injections of sulphates and associated industrial chemicals into the Canadian arctic occurred with a transferral time as short as 5 d from the industrial source. It is therefore no surprise that on a day-to-day basis we often observed great differences between storm events for all chemical species (hence the high variance associated with mean concentrations in Tables 2 and 3). Reliable averages for precipitation chemistry at Saqvaqjuac would therefore probably require a decade, and for the detection of long-term trends, several decades.

Element Runoff: Meadow Watershed

Water discharge from the Meadow watershed ranged from about 1900 to 3900 $m^3 \cdot ha^{-1} \cdot yr^{-1}$ over 4 yr, with 1980 being very wet and 1981 being very dry (Table 7). Solute runoff patterns from terrestrial watersheds at Saqvaqjuac are different from low-latitude runoff patterns where there is no permafrost. Temperate watersheds characteristically have annual major ion outputs which are functions of annual discharge (Likens et al. 1977), because solute concentrations vary far less than instantaneous flow rates. At the Meadow, the annual output of Cl was closely correlated with annual discharge, but Ca, Mg, SO_4, Si, K, and Na all showed small to very large increases in output in 1980 compared with that expected from years with lower discharge (Fig. 5).

Solute concentrations at lower latitudes also tend to be predictable functions of flow rate. Singh and Kalra (1984) found correlation coefficients (r) of 0.38–0.99 for linear fits of yield versus stream flow for Ca, Mg, Na, K, HCO_3, SO_4, and SiO_2 at Marmot Creek, Alberta. A quadratic fit improved the relationships to 0.95 or better for the same components. Lewis and Grant (1979) also found strong correlations between concentration and discharge at Como Creek, Colorado, an area underlain by granitic parent material with no carbonates present. On other granitic watersheds, correlations between element concentration and water discharge have been poorer

TABLE 7. Element discharge from terrestrial watersheds.

Watershed	Year	Mean pH	H ($g \cdot ha^{-1}$)	($kg \cdot ha^{-1}$) SO_4	Cl	K	Mg	Ca	Si	Na	$g \cdot ha^{-1}$ TP	TN	Water ($m^3 \cdot ha^{-1}$)
Meadow													
(15.4 ha)	1978	6.6	0.70	9.75	15.86	1.980	2.06	21.33	1.71	8.76	35	0.96	2938
	1979	7.1	0.18	—	—	1.490	1.89	16.94	0.61	7.05	16	0.70	2163
	1980	7.3	0.22	40.76	21.99	3.530	6.44	65.78	5.50	16.09	16	1.18	3955
	1981	6.7	0.38	9.46	10.07	1.270	1.54	15.60	0.89	5.61	23	0.70	1897
P & N													
(28.6 ha)	1979	6.6	0.46	—	—	1.140	1.21	6.56	1.18	4.15	17	0.73	1948
	1980	—	—	13.19	13.79	2.100	3.16	10.62	4.21	11.00	19	1.32	3380
	1981	6.2	1.52	5.65	7.25	1.390	1.47	7.08	1.06	4.51	25	1.03	2352
Far													
(16.6 ha)	1979	6.5	0.52	—	—	0.480	1.22	4.20	0.89	2.99	22	0.53	1616
	1980	—	—	20.63	19.01	2.280	4.06	22.33	4.30	14.54	27	1.63	4533
	1981	5.8	5.91	5.17	8.21	0.940	1.56	5.50	0.81	6.17	40	1.34	3645
Spring													
(57.6 ha)	1979	—	—	—	—	0.940	1.07	5.75	0.52	5.73	8	0.47	1421
	1980	—	—	13.43	23.22	2.580	3.44	16.54	2.17	16.73	16	1.01	3062
	1981	6.2	1.39	5.48	17.29	1.560	1.75	7.72	0.73	10.58	13	0.78	2312
Jade													
(27.9 ha)	1980	—	—	15.76	13.67	1.760	2.66	18.80	4.10	10.14	25	1.15	3311
	1981	5.9	2.82	4.83	8.70	0.970	1.26	5.66	0.80	3.70	24	0.95	2346
Saqvaqjuac River													
(607 km^2)	1978	—	—	—	—	—	—	—	—	—	—	—	2490[a]
	1979	—	—	—	—	—	—	—	—	—	—	—	1410[a]
	1980	—	—	—	—	—	—	—	—	—	—	—	3060[a]
	1981	6.5	0.59	3.81	4.86	0.77	1.00	6.09	0.65	3.29	8	0.62	1880

[a]Calculated from Dalton (1981).

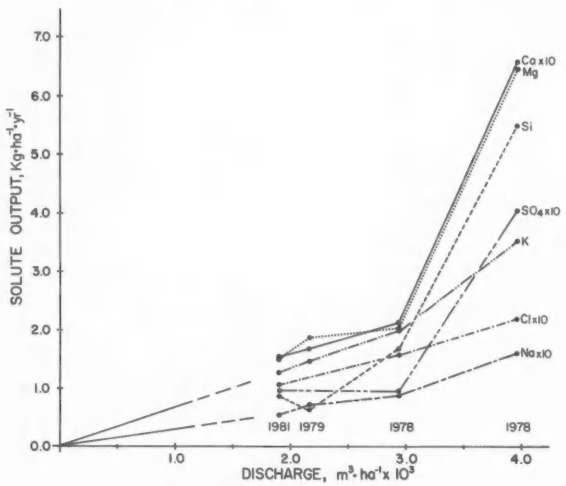

FIG. 5. Areal solute output as a function of total annual discharge for the Meadow watershed, 1978–81. Solute outputs are $kg \cdot ha^{-1} \cdot yr^{-1}$ K, Mg, and Si and $kg \cdot ha^{-1} \cdot yr^{-1} \times 10$ for SO_4, Cl, Ca, and Na. Almost no rain fell in midsummer 1981, whereas very heavy rains fell in August 1980.

(Schindler et al. 1976, at ELA, on Precambrian gneiss; Johnson and Swank 1973, at Coweeta, on Precambrian gneiss; Likens et al. 1977, at Hubbard Brook, on metamorphosed sedimentary rocks).

TABLE 8. Relationship between chemical concentration and log discharge for the Meadow watershed, 1978–81. Concentration = b log discharge ($m^3 \cdot d^{-1}$) + a.

Element	N	b	a	R^2	Probability of slope not different from zero
Na ($mg \cdot L^{-1}$)	146	−2.7	11.06	0.26	0.0001
Cl ($mg \cdot L^{-1}$)	124	−6.09	22.31	0.21	0.0001
SO_4 ($mg \cdot L^{-1}$)	124	−7.92	28.52	0.23	0.0001
Ca ($mg \cdot L^{-1}$)	149	−4.13	20.10	0.16	0.0001
Mg ($mg \cdot L^{-1}$)	149	−0.68	2.80	0.29	0.0001
K ($mg \cdot L^{-1}$)	149	−0.33	1.71	0.10	0.0001
TP ($\mu g \cdot L^{-1}$)	108	—	—	0.0003	0.85
TN ($\mu g \cdot L^{-1}$)	86	—	—	0.01	0.33
PP ($\mu g \cdot L^{-1}$)	148	—	—	0.005	0.40
PN ($\mu g \cdot L^{-1}$)	158	—	—	0.003	0.48

At Saqvaqjuac, we did not find high correlations between discharge and concentration. Correlation coefficients (R^2) for the Meadow watershed ranged from 0.10 to 0.29 for regressions of major ion concentrations on log discharge (Table 8). The slopes for major ions were all negative and highly significant, with concentration decreasing with increasing flow. Hubbard Brook Experimental Forest data showed a negative correlation between flow and concentration for Ca, Mg, and Na and a positive correlation between flow and concentration for K, attributed to the higher biological activity of that element (Likens et al. 1977). Lewis and Grant (1979) found negative

correlations between stream flow and concentrations of Ca, Mg, and HCO_3, with positive correlations for Cl and SO_4 in Como Creek.

One of the most important results of the Saqvaqjuac study was the discovery that great year-to-year variability in solute output from a permafrost watershed is caused by the timing and magnitude of runoff. In a year with little mid- to late summer rainfall, when most runoff comes from snowmelt early in the summer before the active (thawed) layer is well developed, there is generally low solute output from a watershed. In a year with high rainfall in mid- to late summer, when the active zone is well developed, there is high solute output from a watershed.

We were fortunate that 1980 was the wettest, and 1981 the second driest, summer on record at Chesterfield Inlet, so can contrast the behavior of elemental solutes under these two annual flow regimes, using Si and Cl as the two extremes. Silica concentrations were low during snowmelt, gradually increasing 30-fold by mid-August each year (only 1980 and 1981 shown; Fig. 6 and 7). In (dry) 1981, little rain fell in late summer, so total annual Si discharge was low, 0.89 $kg \cdot ha^{-1}$ (Table 7), whereas in (wet) 1980, the heavy rains of late summer interacted with high concentrations of dissolved Si to give an annual output of 5.50 $kg \cdot ha^{-1}$ (Table 7), 6 times higher than for 1981. The Si discharge for the June melt in 1980 was only 12% of the annual total Si discharge.

Conversely, Cl concentrations were high at the onset of snowmelt but dropped rapidly, gradually reaching a minimum 30–40 d after the beginning of melt, and gradually increasing again to high levels in late summer (Fig. 6 and 7). With this seasonal concentration pattern, the annual Cl output covaried closely with total water discharge. The total Cl output for 1980 was only 2.18 times as much as in 1981, compared with a 2.08 difference in water discharge (Table 7).

The other major elements showed seasonal concentration patterns which graded between the two extremes: Si with virtually no early peak concentration, minimum concentration reached the first several days of runoff, and rapidly rising concentrations to very high levels in midsummer, and Cl, with a high early concentration, a gradual drop to minimum concentration early in July, and a gradual rise in late summer. The gradient in concentration pattern was $Cl \rightarrow Na \rightarrow K \rightarrow Mg \rightarrow SO_4 \rightarrow Ca \rightarrow Si$. This gradient was paralled by the range in annual output for each element, with Cl having the lowest range (2.2) and Si the highest (9.1) (derived from Table 7). This same element gradient applies to the sources of elements. Atmospheric input is an important component of Cl runoff, and rock weathering contributes virtually no Cl, whereas Si derives almost entirely from rock and soil weathering and negligible quantities enter the Meadow watershed from the atmosphere. Souces of Na, K, Mg, SO_4, and Ca fall on the gradient between Cl and Si. Sulphate deserves special notice because on dry years about one fourth of the discharge was equalled by precipitation input whereas in 1980 precipitation could have supplied less than 4%, suggesting either a major source deep in the active layer, or accumulation of atmospheric SO_4 in the soil on dry years, or both.

The interaction between surface ice, the active zone, snowmelt, and precipitation combine to give these patterns of seasonal solute concentration and annual discharge. The initial high concentration peaks exhibited by some solutes, particularly those with significant atmospheric inputs such as Cl, Na, K, and P (Fig. 6 and 7), occur when the soil and surface vegetation are frozen. In the arctic, early meltwater accumulates at the ground surface below the snowpack and refreezes as basal ice (Woo and Heron 1981; Woo et al. 1982). Basal ice forms a continuous layer a few millimetres to several centimetres thick over much of the Meadow watershed, and the initial stream channel is ice-floored as well (pers. obs. and Dalton 1981). This basal ice layer must greatly reduce the interaction between waterborne solutes and the soil/plant cover, contributing to the high initial solute discharge for elements with a significant input via winter snowfall, and resulting in minimum concentrations after the melting snowpack has been depleted of the solute but before the soil begins to thaw. In (dry) 1981, 89% of the summer's runoff occurred in June, while the ground was still frozen.

We further explore the relationship between concentration and discharge for Na and SO_4 (Fig. 8). First, the rapid drop in concentration at the onset of melt, and the subsequent increase in concentrations as runoff diminished, resulted in weak negative correlations between concentrations and water discharge (Table 8). Second, solute concentrations were very high in August when the active zone was at maximum thickness. If no rain occurred, as in 1981, concentrations remained high, much higher than at equivalent stream flow rates early in the melt season. If rain did occur, as in 1980, concentrations were lowered but were still much higher than at equivalent flow rates early in the season.

Phosphorus and N behaved differently from the major elements (Fig. 6 and 7). Phosphorous began with an initial high peak the first 2 wk of runoff, suggesting that snowborne P was highly mobile and lost rapidly during spring melt. For the remainder of the summer, P concentrations fluctuated around a constant value which appeared to be independent of instantaneous water discharge. However, annual TP output was not a function of total water discharge; in fact, wet 1980 had the lowest TP output of any year (Table 7), but given the high variance associated with TP concentration measurements, we attach little significance to that fact.

Nitrogen showed only a hint of an early melt peak, which is surprising since relatively large quantities came in with snowfall (Table 3). Concentrations fluctuated around 0.3 $mg \cdot L^{-1}$ regardless of discharge rate, so TN output was a function of water discharge (Table 7). About as much N came in with precipitation as left the watershed, but N-fixation and denitrification were not measured, so output cannot be directly related to input. Although the absence of late-season P and N concentration increases suggests that sources are not deep in the soil, the high biological activity of P and N in soil and vegetation may regulate watershed output by retaining these elements. In temperate, tree-covered watersheds, nutrients (particularly K and NO_3) undergo marked seasonal concentration charges as a result of changing demand from the heavy vegetation cover (Likens et al. 1977). No such pronounced seasonality was found for TN, TP, or K at Saqvaqjuac.

Element Runoff: Watersheds with Lakes

Both hydrological and chemical budgets for lake drainages were less precise than for the Meadow, where all output went through a weir. Water budgets were also more accurate for P & N and Far lakes than for Spring and Jade lakes (Dalton 1981).

Solute concentration and discharge patterns for the terrestrial portion of each lake's watershed were similar to those for the Meadow as typified by the concentration of K in P & N Lake

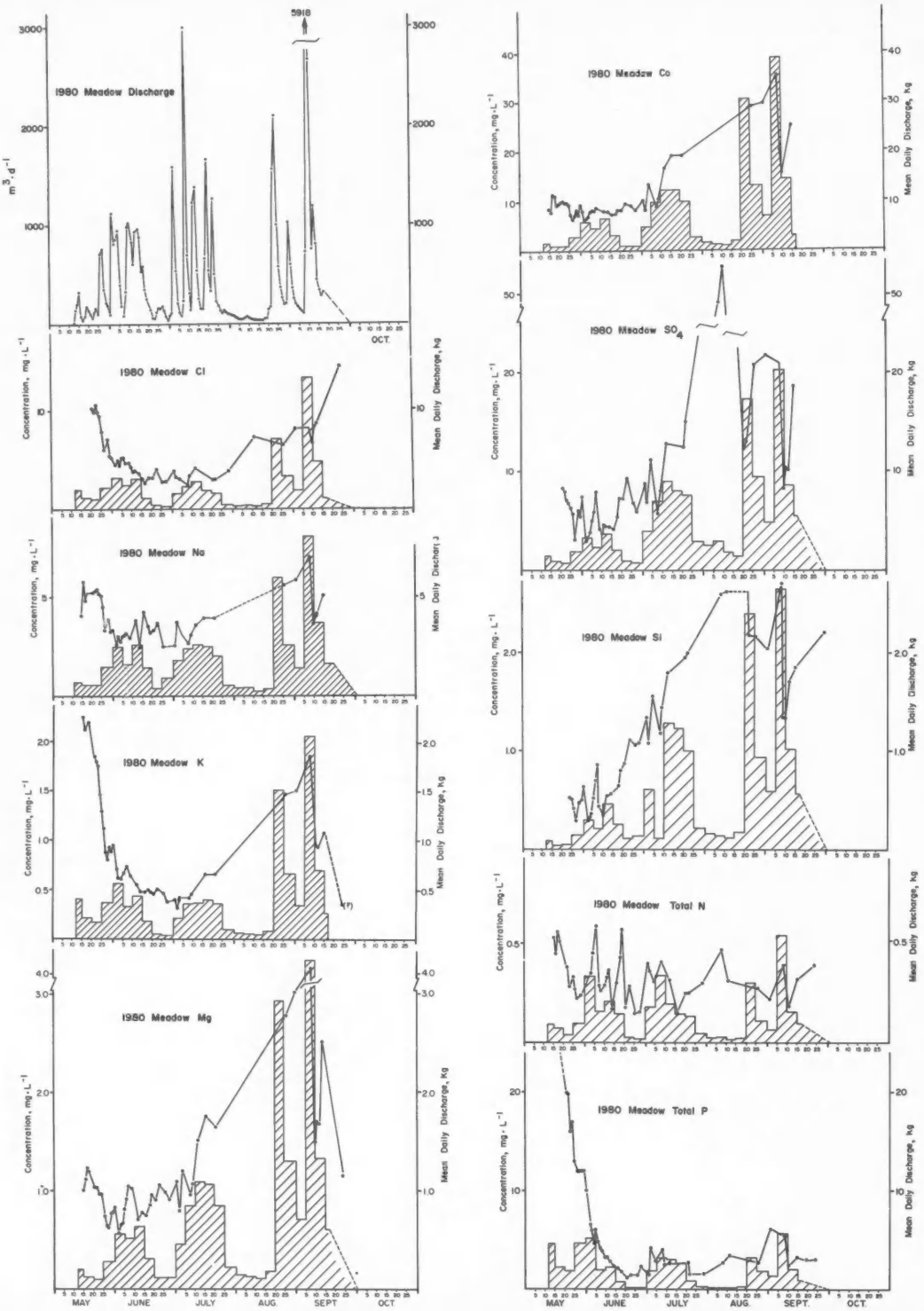

FIG. 6. Water and element discharge from the Meadow watershed, 1980. Shaded bars are mean daily discharge calculated on a daily basis and averaged by week. Lines are concentrations.

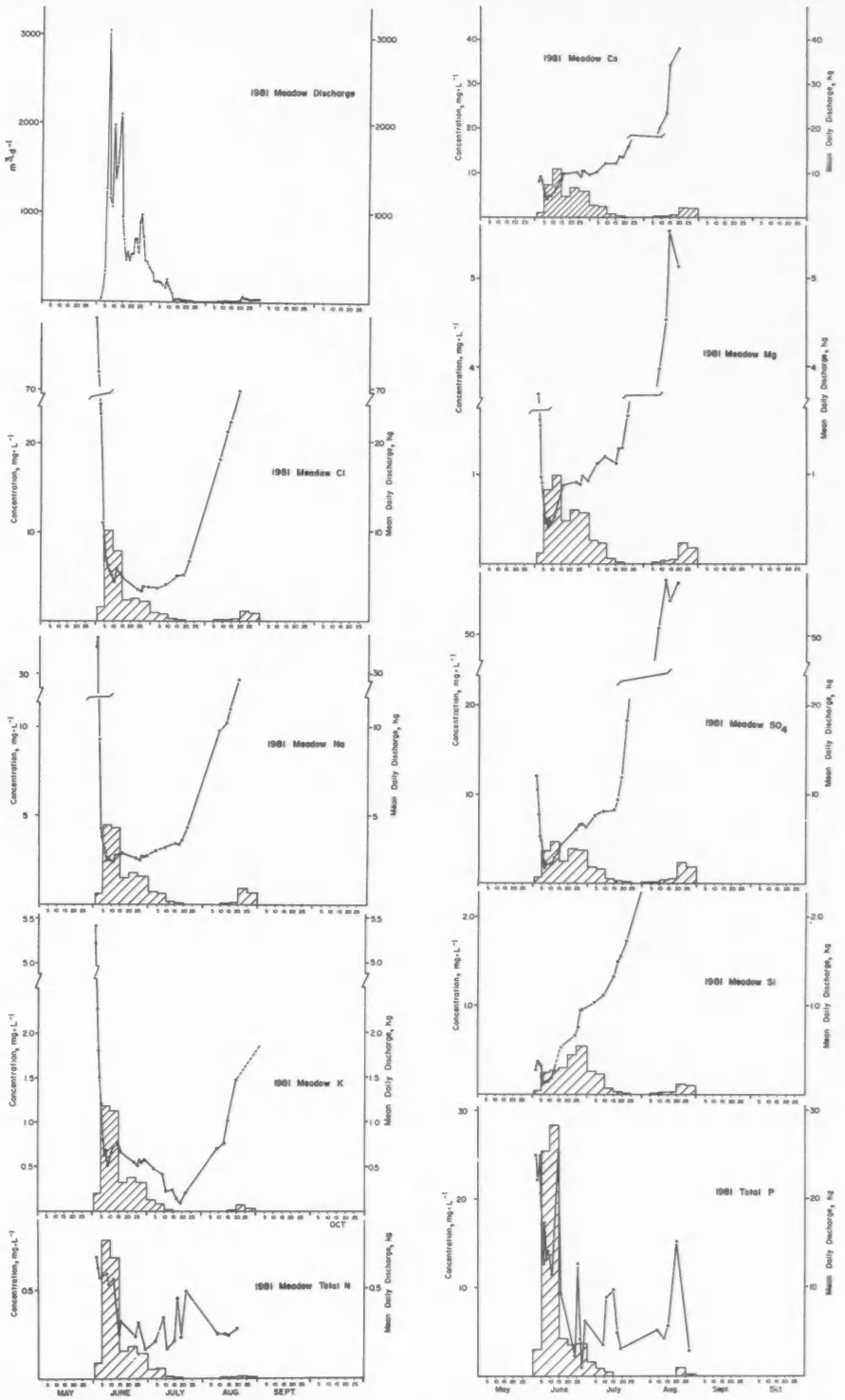

FIG. 7. Water and element discharge from the Meadow watershed, 1981. Shaded bars are mean daily discharge calculated on a daily basis and averaged by week. Lines are concentrations.

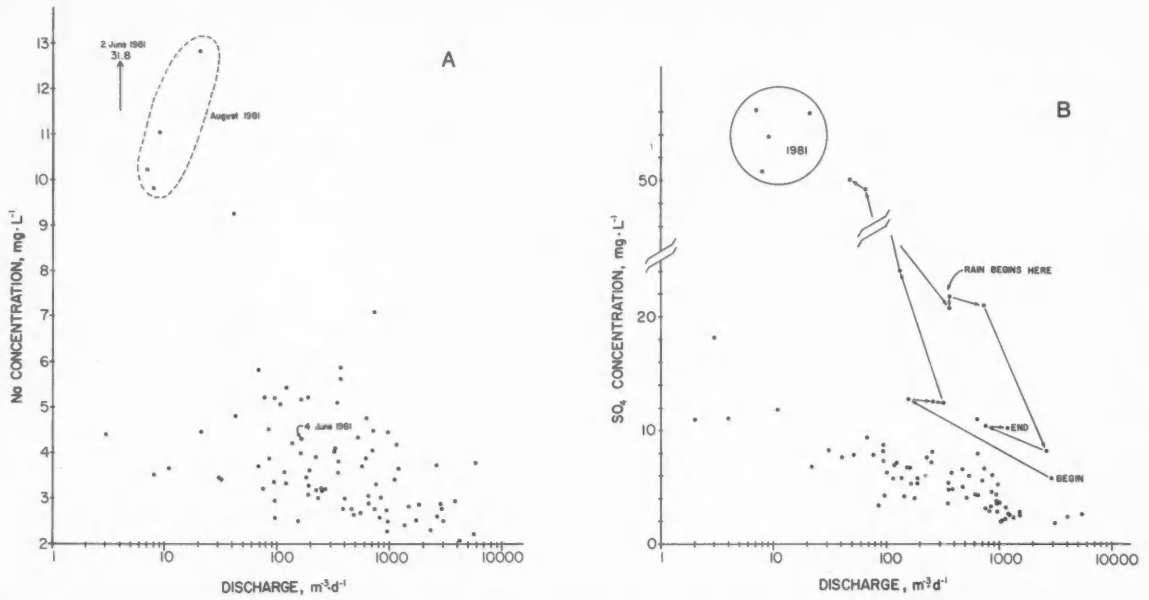

FIG. 8. (A) Sodium and (B) SO_4 concentration versus flow rate for the Meadow watershed, 1978–81. Because the objective of the sampling program was to measure the total element output, the frequency of sampling was largely a function of discharge. If the data were distributed evenly over time, there would be many more points in the low discharge – high concentration area of the graph corresponding to late summer low flows.

inflows in 1980 (Fig. 9). However, the initial descending limb of high concentration early in the melt season was often poorly or not at all developed, and the ascending limb in late summer was also less well developed. This was an artefact of the combination of data from four to eight small and mostly temporary inflows, each of which began to flow, and dry up, at different times, blurring the peaks associated with such inflow. Because we only sampled surface flow, it is also possible that we underestimated late summer inflowing solute concentrations, when unknown amounts of runoff entered the lakes as subsurface flow through the active zone, but we think this error was minor.

Headwater lakes modified seasonal solute concentration patterns, typified by K concentrations in P & N Lake outflow in 1980 (Fig. 9). Lake outflows began a few days after inflows because of snow blockage at the outlets. Outflow solute concentrations were variable because of the complex interaction between the inflowing solute, dilution by lake icemelt, and mixing with lake water (Bergmann and Welch 1985). After ice out, solute concentrations were essentially the same as lake concentrations (Fig. 9). The nutrient elements P, N, and Si were retained by the lakes to varying degrees, which resulted in very different outflow concentrations relative to inflow concentrations for these elements.

Spring Lake drainage had much higher sea salt derived ions than P & N Lake, Far Lake and the Saqvaqjuac River (Table 7). Runoff of Si appeared to be independent of watershed location (Table 7). Phosphorus output was highest from Far Lake drainage (Table 7), and showed no consistent seasonal runoff pattern (not shown). Although each of the lake drainages contributed different quantities per unit area of land surface, element supply to the lakes was largely determined by $A_D:A_0$ (see Table 1), such that Spring Lake generally had the highest areal supply and Far Lake the lowest (Tables 9–12).

Because direct precipitation on the four lakes averaged less than 10% of total water loading, and most elements were less concentrated in precipitation than in land runoff, direct chemical input to the lakes' surfaces by precipitation was only a few percent of the total (Tables 9–12). Hydrogen ion was the sole exception, with up to 90% of the total H input coming from precipitation falling directly on the lakes.

Solute concentrations in the Saqvaqjuac River were much less variable than concentrations in terrestrial watersheds or outflows from headwater lakes. Conservative elements showed only a small smoothly falling early peak, typified by Na and Ca (Fig. 9). River concentrations of P, N, H, and Si all decreased during the summer, typified by Si (Fig. 9), probably as a result of retention by the lake chain.

Water yield from the Saqvaqjuac River watershed averaged only 91% of the water yield from the Meadow (Table 6), probably as a result of increased evaporation from the numerous lakes, as well as possible precipitation differences. Discharges were similar for the two watersheds in 1981, the only year with chemical data for the river, 0.189 m for the Meadow, and 0.188 m for the river (Table 6). The output of all dissolved solutes except H was lower for the river. Total P, TN, Si, and probably SO_4 to some extent were being retained by the lake system. However, the conservative elements Cl, Mg, and Na, as well as K and Ca, had outputs that were only one third or less than the Meadow output. One reason might be that the river watershed receives less sea salt from the atmosphere than the Meadow. Evidence for this is the fact that the output of Na and Cl, but not other elements, was even higher for the Spring Lake drainage than for the Meadow (Table 7). Spring Lake is surrounded on three sides by the sea and would be expected to have more sea salt flux. However, Table 13 shows that sea salt input via precipitation must have been less than 20% of the

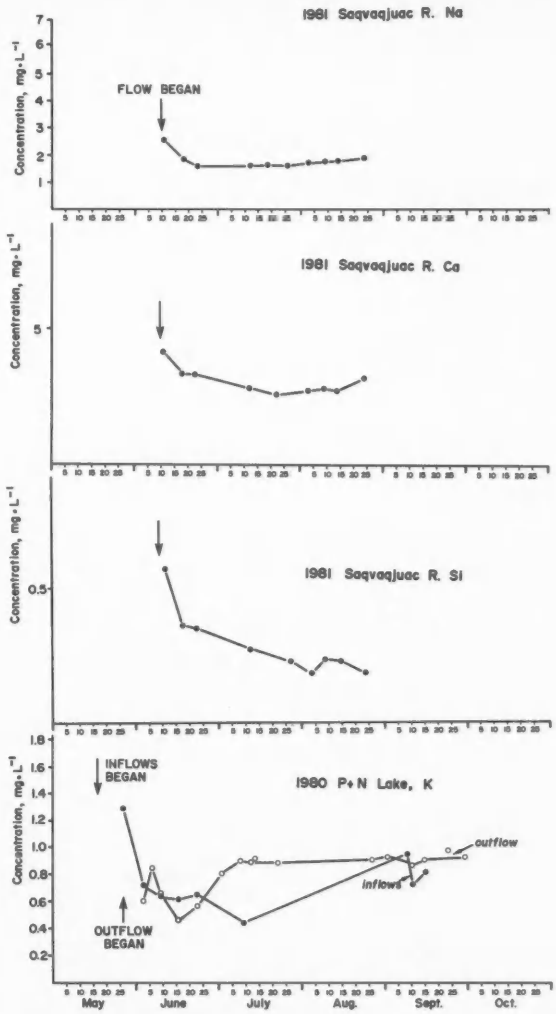

FIG. 9. Sodium, Ca, and Si concentrations in the Saqvaqjuac River, 1981, and K concentrations in P & N Lake inflows and outflow, 1980.

ouput from the Meadow, so unless there is a large atmospheric flux of particulate sea salt near the coast that we did not sample in our bulk precipitation collector, which is highly unlikely, differential atmospheric input cannot account for the low flux of conservative elements from the river.

We suspect rather that Cl, Na, Ca, Mg, K, and SO_4 remain in the soil as residues from marine inundation and are being slowly washed out into terrestrial runoff as the land rises isostatically from the weight of the Wisconsinan glaciation. From Table 7 we see that for 1981 the Cl output differentials between the Saqvaqjuac River and the coastal watersheds Meadow and Spring Lake were on the order of 10 $kg \cdot ha^{-1}$. If half the land surface has an active zone of ≈ 1 M at an average soil moisture content of, say, 30%, it would hold about 5000 kg $Cl \cdot ha^{-1}$ if the solution were sea water, or enough Cl to last 500 yr at an output of 10 $kg \cdot ha^{-1} \cdot yr^{-1}$. Of course the actual washout sequence is much more complicated, but we present the calculation to show that residual sea salt could account for both the differences between the river and the coastal watersheds and the very high Cl outputs of the coastal watersheds relative to the atmospheric Cl input (Table 13).

Comparative Chemical Budgets

Here we compare the yield of water and chemicals from the Saqvaqjuac drainages with those from two comparable drainages at lower latitudes, the Rawson Lake drainage at the Experimental Lakes Area (ELA) in northwestern Ontario and Hubbard Brook Experimental Forest (HBEF) in north-central New Hampshire. Like Saqvaqjuac, the bedrock of ELA is Precambrian granite overlain by granitic glacial deposits (Schindler et al. 1976). Watersheds 1–6 at HBEF are underlain by highly metamorphosed granitic deposits of the Littleton formation, overlain by glacial deposits derived locally from the Littleton formation (Likens et al. 1977). The bedrock of all three areas has almost no calcareous material. Saqvaqjuac differs mainly from ELA and HBEF in that temperatures are lower, permafrost is present, vegetation cover is much less, and it is on the sea coast. It is a coastal ELA with permafrost instead of trees.

Water input from precipitation is much less at Saqvaqjuac, about 0.3 m compared with 0.8 and 1.3 m at ELA and HBEF (Table 13). Of this, very little is lost as evapotranspiration or storage at Saqvaqjuac, whereas about one third at HBEF and two thirds at ELA is lost before it leaves as stream flow. This difference must result largely from the differences in plant cover and resultant evapotranspiration. However, winter precipitation is notoriously difficult to measure in the Arctic, and the redistribution of snow by wind profoundly alters local snow accumulations. The mean water equivalent for early spring (premelt) snow cover in the Meadow drainages basin was 1416 $m^3 \cdot ha^{-1}$ in 1978 and 966 $m^3 \cdot ha^{-1}$ in 1979 (Dalton 1981). We found winter precipitation to be 1610 and 1020 $m^3 \cdot ha^{-1}$ over the same period (Table 4), so the mean measured snow cover was 91% of measured snow fall for the 2 yr. We therefore assume that the redistribution of snowfall by wind did not greatly alter the mean snow cover in the Meadow basin from that calculated from winter snowfall.

Hydrogen ion input is similar at ELA and the Meadow, whereas HBEF has much higher inputs and outputs. Sulphate output by the Meadow is intermediate between ELA and HBEF. Silica outputs are very low at Saqvaqjuac compared with ELA and HBEF, which we assume results from lower precipitation and slower rates of chemical weathering due to low temperature and permafrost. For the major ions, the Meadow is nowhere close to having balanced inputs and outputs. ELA and HBEF both lose Mg, Ca, Na, and K and retain Cl. The Meadow, however, loses very much more of all the major ions, including Cl and SO_4, than comes in via the atmosphere (cause discussed below).

More TP and TN are also lost from the Meadow than came in. This is unusual for N, which tends to be retained by terrestrial watersheds (Table 13; Likens et al. 1977).

Lake Annual Supply Rates and Retention

Hydrogen was the ion retained most efficiently by the lakes, with retention averaging 90% and being over 99% in some lake years (e.g. P & N Lake, 1979, Table 14). Under natural conditions, Si was retained with second-greatest efficiency, averaging 76%. Total P supply per unit area of lake surface for headwater lakes at Saqvaqjuac was higher than at Char Lake (74°42′N) and slightly lower than Lake Stugsjön (68°27′N) and

TABLE 9. P & N Lake element supply (kg·ha lake surface^{-1}). Dissolved fractions only except fo

	H (g·ha^{-1})	SO_4	Cl	K	Mg	Ca
1978						
Σ Input	—	251.0	48.0	6.50	6.63	36.5
% from precipitation	—	6	4	>1	1	1
1979						
Input, ice-on	6.8	—	—	3.86	3.91	20.9
Outflow, ice-on	0.6	—	—	4.29	5.73	28.3
Input, ice-off	101.5[a]	—	—	0.78	1.14	6.0
Outflow, ice-off	0.0	—	—	0.07	0.08	0.4
Σ Input	108.2[a]	—	—	4.64	5.05	26.9
Outflow	0.5	—	—	4.36	5.81	28.7
% retention	>99	—	—	6	−15	−7
% from precipitation	84[b]	—	—	<1	3	1
1980						
Input, ice-on	—	14.6	15.3	3.78	3.06	16.6
Outflow, ice-on	—	9.3	21.1	2.79	3.48	14.6
Input, ice-off	—	39.9	43.2	5.13	9.93	26.8
Outflow, ice-off	—	25.5	55.5	7.45	10.30	36.5
Σ Input	—	54.5	58.5	8.91	12.99	43.4
Σ Outflow	—	34.9	76.4	10.24	13.78	51.1
% retention	—	36	−31	−15	−6	−18
% from precipitation	—	2	5	<1	2	1
1981						
Input, ice-on	14.6	19.7	26.4	5.02	4.49	24.0
Outflow, ice-on	3.4	16.2	29.7	4.37	4.78	19.4
Input, ice-off	103.4[a]	3.8	3.3	0.66	1.51	4.7
Outflow, ice-off	0.1	1.5	2.7	0.42	0.49	2.3
Σ Input	118.0[a]	23.5	29.7	5.68	6.00	28.7
Σ Output	3.5	17.7	32.4	4.79	5.27	21.7
% retention	97	25	−9	16	12	24
% from precipitation	70[b]	4	3	<1	<1	<1
Mean summer concentration (mg·L^{-1})	7.19 pH	2.88	6.68	0.91	1.19	5.40

[a] Includes 686 mol H added as H_3PO_4.
[b] Of natural loading.
[c] Includes 21.0 kg Na and 12.8 kg N·ha^{-1} added as $NaNO_3$.
[d] Includes 18.0 kg Na and 11.0 kg N·ha^{-1} added as $NaNO_3$.
[e] Includes 1.0 kg P·ha^{-1} as H_3PO_4.
[f] Includes precipitation and snowmelt on the lake surface.

except for P, N, and C; n = natural, f = fertilizer.

Ca	Si	n Na	$n+f$ Na	n TP	$n+f$ TP	n TN	$n+f$ TN	TOC	H_2O (vert. m)[f]
		26.7	—	0.154	—	5.23	—	—	1.39
36.5	8.56	2	—	3	—	10	—	—	11
1	<1								
20.9	3.31	13.2	13.2	0.067	0.067	2.81	2.81	—	0.75
28.3	3.23	23.0	23.0	0.050	0.050	2.13	2.13	—	0.59
6.0	1.44	4.2	25.2[c]	0.015	1.015[e]	0.45	13.25[c]	—	0.15
0.4	0.03	0.3	0.3	<0.001	<0.001	0.03	0.03	—	0.01
26.9	4.75	17.4	38.4[c]	0.082	1.082[e]	3.26	16.06[c]	—	0.90
28.7	3.26	23.3	23.3	0.050	0.050	2.19	2.19	—	0.60
−7	31	—	39	—	95	—	86	—	33
1	<1	4[b]	—	<1[b]	—	10[b]	—	—	13
16.6	2.86	12.4	12.4	0.036	0.036	1.96	1.96	—	0.48
14.6	0.47	16.8	16.8	0.031	0.031	2.00	2.00	—	0.46
26.8	14.13	33.3	63.7[d]	0.090	1.090[e]	3.96	14.96[d]	—	1.15
36.5	1.50	45.3	45.3	0.086	0.086	3.99	3.99	—	0.84
43.4	16.99	45.7	76.1[d]	0.126	0.126[e]	5.92	16.92[d]	—	1.63
51.1	1.97	62.1	62.1	0.117	0.117	5.99	5.99	—	1.30
-18	88	—	18	—	90	—	65	—	20
1	<1	3	—	13	—	10	—	—	10
24.0	3.05	15.9	15.9	0.099	0.099	4.09	4.09	58.5	0.94
19.4	0.80	22.8	22.8	0.075	0.075	3.31	3.31	39.6	0.90
4.7	1.24	3.5	21.5[d]	0.010	1.010[e]	0.47	11.47[d]	6.1	0.12
2.3	0.89	2.4	2.4	0.004	0.044	0.17	0.17	2.6	0.05
28.7	4.29	19.4	37.4[d]	0.109	1.109[e]	4.56	15.56	64.6	1.06
21.7	1.69	25.2	25.2	0.079	0.079	3.48	3.48	42.2	0.95
24	61	—	33	—	93	—	78	35	10
<1	<1	6	—	8	—	8	—	—	−16
5.40	0.236	—	5.13	—	0.011	—	0.367	6.0	—

TABLE 10. Far Lake element supply (kg·ha lake surface^{-1}). Dissolved fractions only, except for P,

	H (g·ha^{-1})	SO_4	Cl	K	Mg	Ca
1978						
Input	—	25.6	59.9	4.38	7.43	26.1
% from precipitation	—	<7	3	<1	1	1
1979						
Input, ice-on	6.4	—	—	1.49	3.19	17.2
Outflow, ice-on	0.9	—	—	3.46	4.35	19.6
Input, ice-off	97.3[a]	—	—	0.68	2.27	1.6
Outflow, ice-off	0.0	—	—	0.27	0.43	1.4
Σ Input	103.7[a]	—	—	2.16	5.46	18.8
Σ Outflow	0.9	—	—	3.73	4.78	21.1
% retention	99	—	—	−73	12	−12
% from precipitation	70[b]	—	—	1	3	2
1980						
Input, ice-on	—	14.7	14.7	1.57	2.19	10.2
Outflow, ice-on	—	8.9	28.9	2.16	3.35	10.9
Input, ice-off	—	79.1	73.4	8.73	16.30	90.5
Outflow, ice-off	—	33.2	99.1	7.68	13.05	47.4
Σ Input	—	93.8	88.1	10.30	18.49	100.7
Σ Output	—	42.1	128.0	9.84	16.40	58.3
% retention	—	55	−45	4	13	42
% from precipitation	—	1	3	<1	1	<1
1981						
Input, ice-on	37.0	18.1	28.7	4.00	5.13	17.4
Outflow, ice-on	7.7	20.8	61.6	5.86	7.32	28.2
Input, ice-off	110.4[a]	7.0	9.35	0.32	1.95	7.7
Outflow, ice-off	0.3	3.8	10.9	0.92	1.41	5.6
Σ Input	147.4[b]	25.1	38.1	4.32	7.08	25.0
Σ Outflow	8.0	24.7	72.5	6.78	8.73	38.8
% retention	94	2	−91	−57	−23	−35
% from precipitation	39[b]	6	3	2	1	2
Mean summer concentration (mg·L^{-1})	6.98 pH	1.89	7.80	0.56	0.91	3.2

[a] Includes 1.0 kg P and 0.1 kg H·ha^{-1} added as H_3PO_4.
[b] Of natural H input only.
[c] Includes precipitation and snowmelt on the lake surface.

pt for P, N, and C; n = natural, f = fertilizer.

Ca	Si	Na	n TP	$n + f$ TP	TN	TOC	H_2O (vert. m)[c]
26.1	7.27	21.6	0.280	—	5.81	—	1.53
1	<1	3	2	—	10	—	13
17.2	2.00	9.16	0.074	0.074	2.22	—	0.61
19.6	0.65	27.8	0.050	0.050	1.89	—	0.66
1.68	2.00	4.54	0.026	1.026	0.73	—	0.17
1.43	0.03	2.27	0.005	0.005	0.11	—	0.05
18.8	4.00	13.7	0.100	0.100	2.95	—	0.78
21.1	0.68	30.1	0.056	0.056	2.00	—	0.70
−12	83	−120	—	95	32	—	13
2	<1	4	13	—	24	—	7
10.2	2.27	10.1	0.036	0.036	2.27	—	0.58
10.9	0.70	19.8	0.025	0.025	1.22	—	0.57
90.5	17.03	56.4	0.099	1.099[a]	5.65	—	1.74
47.4	3.00	64.0	0.106	0.106	3.65	—	1.44
100.7	19.30	66.5	0.135	1.135[a]	7.92	—	2.31
58.3	3.70	83.9	0.135	0.131	4.86	—	2.01
42	81	−26	—	92	39	—	13
<1	<1	2	9	—	7	—	12
17.4	2.57	23.8	0.172	0.172	5.95	85.8	1.58
28.2	0.95	36.0	0.212	0.212	6.95	74.0	1.50
7.7	1.05	6.1	0.012	1.012[a]	0.57	9.7	0.18
5.6	0.13	7.4	0.022	0.022	0.49	6.6	0.17
25.0	3.62	29.8	0.184	1.184[a]	6.51	95.5	1.76
38.8	1.08	43.4	0.234	0.234	7.43	80.6	1.67
−35	70	−45	—	80	−14	16	5
2	<1	5	6	—	8	—	7
3.27	0.160	4.86	—	0.014	0.29	4.06	—

TABLE 11. Spring Lake element supply (kg·ha lake surface^{-1}). Dissolved fractions

	H (g·ha^{-1})	SO_4	Cl	K	Mg
1979					
Input, ice-on	5.9	—	—	6.72	7.57
Outflow, ice-on	0.7	—	—	12.13	14.78
Input, ice-off	5.8	—	—	1.14	1.51
Outflow, ice-off	0.0	—	—	0.80	1.32
Σ Input	11.7	—	—	7.87	9.07
Σ Output	0.7	—	—	12.93	16.10
% retention	94	—	—	−64	−78
% from precipitation	90	—	—	<1	2
1980					
Input, ice-on	—	17.4	51.0	4.94	6.33
Outflow, ice-on	—	14.6	51.1	4.83	4.90
Input, ice-off	—	95.9	145.7	16.84	22.62
Outflow, ice-off	—	62.9	248.1	12.41	29.59
Σ Input	—	113.3	196.7	21.78	28.95
Σ Outflow	—	77.5	299.2	26.24	34.49
% retention	—	32	−52	−21	−20
% from precipitation	—	12	3	<1	<1
1981					
Input, ice-on	23.7	31.6	122.0	11.08	11.56
Outflow, ice-on	4.0	35.7	119.1	10.75	13.30
Input, ice-off	5.8	15.4	22.8	1.91	3.04
Outflow, ice-off	0.2	5.0	25.4	2.30	3.08
Σ Input	29.5	47.0	144.8	12.99	14.60
Σ Output	4.2	40.7	144.6	13.05	16.38
% retention	85	13	±0	±0	−12
% from precipiation	—	2	<1	<1	<2
Mean summer concentration (mg·L^{-1})	7.39 pH	3.23	16.09	1.37	1.91

[a]Includes precipitation and snowmelt on the lake surface.

ractions only, except for P, N, and C.

lg	Ca	Si	Na	TP	TN	TOC	H_2O (vert. M)[a]
7.57	38.2	2.77	41.7	0.068	3.71	—	1.15
4.78	68.5	2.86	116.4	0.060	3.54	—	1.16
1.51	10.1	1.55	6.7	0.010	0.52	—	0.17
1.32	5.7	0.10	9.3	0.003	0.25	—	0.08
9.07	48.3	4.32	48.4	0.078	4.23	—	1.32
6.10	74.2	2.96	125.7	0.063	3.79	—	1.24
3	−53	32	−160	19	10	—	6
2	<1	<1	1	15	6	—	7
6.33	31.8	2.51	33.3	0.070	3.10	—	0.82
4.90	21.1	5.06	34.3	0.091	2.12	—	0.65
2.62	106.8	15.58	106.4	0.071	5.90	—	1.93
9.59	114.9	0.96	186.2	0.091	4.62	—	1.56
8.95	138.6	18.09	139.2	0.141	9.00	—	2.75
4.49	136.1	6.02	220.5	0.125	6.74	—	2.21
0	2	66	−58	12	25	—	20
1	<1	<1	3	12	11	—	7
1.56	51.1	3.14	77.7	0.090	6.20	99.7	1.80
3.30	67.3	2.77	89.3	0.120	7.39	95.3	1.71
3.04	13.6	2.94	12.2	0.032	0.64	11.2	0.21
3.08	12.2	0.41	20.1	0.020	0.88	9.3	0.19
4.60	64.7	6.08	89.9	0.122	6.84	110.0	2.01
6.38	79.5	3.18	109.4	0.140	8.27	104.6	1.90
2	−23	48	−22	−15	−21	6	5
2	<1	<1	1	4	6	—	4
1.91	7.20	0.133	11.7	0.0097	0.361	5.52	—

TABLE 12. Jade Lake element supply (kg·ha lake surface^{-1}). Dissolved fractions only, e

	H (g·ha^{-1})	SO_4	Cl	K	Mg	Ca
1980						
Input, ice-on	—	28.1	26.7	3.83	4.06	26.4
Outflow, ice-on	—	12.0	17.0	3.07	4.65	23.6
Input, ice-off	—	110.3	81.3	9.74	16.67	118.6
Outflow, ice-off	—	35.9	42.4	5.45	10.55	62.4
Σ Input	—	138.4	108.0	13.57	20.73	145.0
Σ Outflow	—	47.9	59.4	8.52	15.20	86.0
% retention	—	65	45	37	27	41
% from precipitation	—	<1	3	≪1	1	<1
1981						
Input, ice-on	32.0	28.4	57.3	6.56	8.25	32.0
Outflow, ice-on	9.3	23.6	38.4	3.82	5.00	25.3
Input, ice-off	15.8	10.5	10.8	1.03	1.58	11.8
Outflow, ice-off	0.3	1.4	2.1	0.27	0.45	2.7
Σ Input	47.8	38.9	68.1	7.59	9.83	43.8
Σ Outflow	9.6	25.0	40.5	4.09	5.45	28.0
% retention	80	36	41	46	45	36
% from precipitation	55	5	2	1	1	<1
Mean summer concentration (mg·L^{-1})	6.50 pH	2.2	3.0	0.40	0.70	4.00

[a] Includes 36 kg Na and 22 kg N·ha^{-1} as $NaNO_3$.
[b] Includes 2 kg P and 0.19 kg H·ha^{-1} as H_3PO_4.
[c] Includes precipitation and snowmelt on the lake surface.

s only, except for P, N, and C; n = natural; f = fertilizer.

Ca	Si	Na	n TP	$n+f$ TP	n TN	$n+f$ TN	TOC	H_2O (vert. m)[c]
26.4	4.18	18.8	0.027	0.027	3.78	3.78	—	0.90
23.6	1.15	21.9	—	0.024	—	3.45	—	0.78
18.6	27.35	60.4[a]	0.130	2.130[b]	5.62	27.62[a]	—	1.65
62.4	0.98	50.4	—	0.060	—	6.31	—	1.52
45.0	31.53	79.2[a]	0.157	2.157[b]	9.40	31.40[a]	—	2.55
86.0	2.13	72.3	—	0.084	—	9.76	—	2.30
41	93	9	—	96	—	69	—	10
<1	≪1	2	8	<1	6	2	—	10
32.0	3.74	24.3	0.177	—	7.07	—	127.4	1.64
25.3	1.83	31.0	0.195	—	6.79	—	159.1	1.98
11.8	6.14	6.23	0.011	—	0.73	—	10.9	0.16
2.7	0.10	2.50	0.010	—	0.35	—	5.9	0.08
43.8	9.88	30.5	0.188	—	7.80	—	138.3	1.80
28.0	1.93	33.5	0.205	—	7.14	—	165.0	2.06
36	80	−9	−9	—	8	—	−19	−14
<1	≪1	7	4	—	6	—	—	6
4.00	0.20	3.70	—	0.018	—	0.500	5.94	—

TABLE 13. Element budgets ($kg \cdot ha^{-1}$) for the Meadow watershed, Saqvaqjuac River, Rawson Lake drainage at the Experimental Lakes Area in northwestern Ontario, and Hubbard brook Experimental Forest in north-central New Hampshire.

Watershed	H	SO_4	Cl	K	Mg	Ca	Si	Na	TP[a]	TN	H_2O (M)
Meadow											
Atmospheric input	0.046	2.4	2.6	—	0.2	0.5	0.0	1.4	0.013	0.82	0.29
Stream output	0.0003	20.0	16.0	2.1	3.0	29.9	2.2	9.4	0.022	0.89	0.27
Balance	0.046	−17.6	−13.4	—	−2.8	−29.4	−2.2	−8.0	−0.009	−0.07	0.02
Saqvaqjuac[b]											
Atmospheric input	0.046	2.4	2.6	—	0.2	0.5	0.0	1.4	0.013	0.82	0.29
Steam output	0.001	3.8	4.9	0.8	1.0	6.1	0.6	3.3	0.008	0.62	0.19
Balance	0.045	−1.4	−2.3	—	−0.8	−5.6	−0.6	−1.9	0.005	0.20	0.10
ELA[c]											
Atmospheric input	0.056	3.3	2.7	1.1	0.9	3.8	0.0	1.6	0.327	6.25	0.80
Stream output	0.010	3.2	0.7	1.3	2.5	6.4	14.2	3.9	0.051	1.01	0.28
Balance	0.046	0.1	2.0	−0.2	−1.6	−2.6	−14.2	−2.3	0.276	5.24	0.52
HBEF[d]											
Atmospheric input	0.96	38.0	6.2	0.9	0.6	2.2	0.0	1.6	—	—	1.32
Stream output	0.10	53.8	4.6	1.9	3.1	13.7	38.4	7.2	19	4.01	0.83
Balance	0.86	−14.8	1.6	−1.0	−2.5	−11.5	−38.4	−5.6	—	—	0.49

[a] 3−4 yr of data from Table 7, 1978−81; input from Table 4.
[b] 1 yr of data from Table 7, 1981; input is assumed to be the same as at Saqvaqjuac Inlet (Table 4).
[c] From Schindler et al. (1976), table 3 (chemical), table 2 (H_2O), for Rawson Lake terrestrial drainage, 342.09 ha, 1970−73.
[d] From Likens et al. (1977), table 11 (chemical), table 1 (H_2O), mean for undisturbed watersheds, 1963−74, except for TP and TN, taken from Likens et al. (1977), table 9, watershed 6, 1966−70 only.

TABLE 14. Percent average annual retention [(1 − outflow)/(inflow)] in Saqvaqjuac lakes and Rawson Lake, ELA (from Schindler et al. 1976). Dissolved fractions only, except for P, N, and C; number of data years in parentheses; mean percent is weighted for number of data years.

	H	SO_4	Cl	K	Mg	Ca	Si	Na	TP	TN	TOC	H_2O
P & N	98 (2)	33 (2)	−23 (2)	−1 (3)	−3 (3)	−3 (3)	73 (3)	27 (3)[a]	93 (3)[a]	76 (3)[a]	35 (1)	21 (3)
Far	96 (2)	44 (2)	−59 (2)	−21 (3)	4 (3)	18 (3)	80 (3)	−43 (3)	88 (3)[c]	18 (3)	16 (1)	10 (3)
Spring	88 (2)	26 (2)	−30 (2)	−22 (3)	−27 (3)	−15 (3)	57 (3)	−64 (3)	4 (3)	6 (3)	6 (1)	12 (3)
Jade	80 (1)	59(2)	43 (2)	40 (2)	32 (2)	40 (2)	90 (2)	4 (2)[b]	88 (2)[b]	57 (2)[b]	−19 (1)	±0 (11)
Mean	92 (7)	41 (8)	−17 (8)	−5 (11)	−1 (11)	7 (11)	74 (11)	—	—	—	9 (4)	12 (11)
Rawson	96 (3)	20 (1)	24 (2)	13 (4)	8 (4)	6 (4)	44 (4)	17 (4)	72 (4)	60 (94)	53 (3)	18 (4)

[a] Artificially high because of H_3PO_4 and $NaNO_3$ addition on all three years.
[b] Artificially high because of H_3PO_4 and $NaNO_3$ addition on one of the two years.
[c] Artificially high because of H_3PO_4 addition on all three years.

TABLE 15. Comparative nutrient supply and rentention ($kg \cdot ha$ lake $surface^{-1}$).

System and source	N lat.	TP input	TP output	TP retention	TN input	TN output	TN retention	Input N:P	Si input	Si output	Si retention
Char Lake (de March 1975)	74°42′	0.025	0.011	0.55	0.325	0.122	0.63	183	—	—	—
P & N Lake (this study)[a]	63°39′	0.106	0.082	0.23	4.58	3.89	0.15	43	8.68	2.31	0.73
Far Lake (this study)[a]	63°39′	0.140	0.140	0.00	5.79	4.76	0.18	41	8.97	1.82	0.80
Spring Lake (this study)	63°39′	0.114	0.109	0.04	6.68	6.27	0.06	59	9.50	4.05	0.57
Jade Lake (this study)[a]	63°39′	0.173	—	—	8.60	—	—	50	20.71	2.03	0.90
Lake Stugsjön (Persson et al. 1975 (summer only))[b]	68°27′	0.079	0.031	0.60	2.27	0.95	0.58	29	—	—	—
Rawson Lake (Schindler et al. 1976)	49°35′	0.645	0.181	0.72	12.63	5.07	0.60	20	90.3	51.0	0.44

[a] Input is natural supply only, whereas output includes the effects of fertilizer P and N; Si budgets, and the N budget for Far Lake, may have been affected as well.
[b] Stugsjön does not include springmelt, which adds TP and TN loading about 2 times the summer-only values given here.

TABLE 16. Element concentrations in lake ice at Saqvaqjuac, 1980–81 (n = 5–6 for each lake; SD = standard deviation; SE = standard error of the mean; % = mean in ice ÷ mean in adjacent water (see Methods for details)).

	Far Lake			P & N Lake			Spring Lake			Jade Lake			All lakes		
Element	$\bar{x}$	SD	%	$\bar{x}$	SD	%	$\bar{x}$	SD	%	$\bar{x}$	SD	%	$\bar{x}$	SE	%
Conductance ($\mu S \cdot cm^{-1}$)	2.49	0.36	4	2.99	0.38	3	3.11	1.05	2	2.95	0.22	3	2.89	0.14	3
K ($mg \cdot L^{-1}$)	<0.02	—	<3	<0.02	—	<2	<0.02	—	<1	<0.02	—	<2	<0.02	—	<2
Mg ($mg \cdot L^{-1}$)	0.29	0.55	23[a]	0.06	0.08	4	0.23	0.28	13[a]	0.01	0.00	<1	0.15[a]	0.07	10[a]
Ca ($mg \cdot L^{-1}$)	0.85	0.93	19	0.19	0.27	3	0.80	1.23	7	<0.05	—	<1	<0.47	—	<5
Na ($mg \cdot L^{-1}$)	<0.03	—	<1	0.15	0.06	3	<0.08	—	<5	0.09	0.01	1	<0.05	—	<2
Cl ($mg \cdot L^{-1}$)	<0.10	—	<1	0.42	0.22	6	<0.10	—	<5	0.22	0.11	4	<0.21	—	<4
SO_4 ($mg \cdot L^{-1}$)	<0.10	—	<3	0.10	0.00	2	<0.10	—	<2	<0.20	—	<4	<0.12	—	<3
TP ($\mu g \cdot L^{-1}$)	2.86	0.74	39	6.17	2.69	62	15.8[a]	18.8	372[a]	3.97	1.68	20	4.33[b]	0.97	40[b]
TN ($\mu g \cdot L^{-1}$)	132	67	43	320	141	63	163	50	35	423	231	49	260	68	47
NO_3 ($\mu g \cdot L^{-1}$)	2.50	0.59	45	3.76	1.18	7	3.22	1.35	71	4.21	0.77	2	3.42	0.37	31
Si ($\mu g \cdot L^{-1}$)	0.58	0.53	≪1	0.11	1.29	≪1	1.57	0.71	≪1	−0.95	2.45	≪1	0.33	0.52	≪1

[a] Includes probable analytical errors and is therefore erroneously high.
[b] Without Spring Lake.

TABLE 17. Importance of lake ice to P and N supply ($mg \cdot m^{-2}$) in Saqvaqjuac lakes, 1981, where internal loading from lake ice = (lakewide mean ice thickness) (0.92) (mean concentration in icemelt from Table 16).

Lake	Natural external TP supply	Internal TP supply from icemelt	Natural external TN supply	Internal TN supply from icemelt	Internal:external TP supply	Internal:external TN supply
P & N	10.9	7.66	456	397	0.70	0.87
Far	18.4	3.58	651	165	0.19	0.25
Spring	12.2	—	684	207	—	0.30
Jade	18.8	5.81	780	619	0.31	0.79

much lower than at Rawson Lake (49°35′N) (Table 15). Phosphorus was retained with 90% efficiency in the three lakes with added P, but Spring Lake retained only about 4% of its natural P loading. Total N supply was high at Saqvaqjuac compared with Char Lake and Lake Stugsjön but was again lower than Rawson Lake. Likewise, a high proportion of N was retained by the N-enriched P & N and Jade lakes, whereas Far and Spring lakes retained only 18 and 20% of naturally loaded N, although N-fixation (M. A. Bergmann and H. E. Welch, unpubl.) and denitrification must also be added to inflows and outflows for complete N budgets. Percent TN retention was very low compared with Char, Stugsjön, and Rawson lakes. The TN:TP ratio for natural supply drops consistently with decreasing latitude from a high of 183 for Char Lake to a low of 20 for Rawson Lake. We are preparing a more detailed analysis of nutrient supply, retention, and Chl.

Sulphate was retained by all lakes, with a mean efficiency of 43%. Calcium was also retained by three of the four lakes. Magnesium input/output was about balanced. Potassium was variable but appeared to have a net loss. Chloride showed very high losses in all but Jade Lake, and Na also underwent high losses in the two lakes with no added $NaNo_3$. Total organic carbon (TOC) data was complete only for one year, 1981, so great significance should not be attached to the figures. It appears that TOC retention was likely (Table 14), with retained amounts ranging from $-2.7\ g \cdot m^{-2}$ in Jade Lake to $+2.2\ g \cdot m^{-2}$ in P & N Lake.

Multiyear averages obscure important differences in annual loading and retention which occured at Saqvaqjuac. In 1981 the retention of H, SO_4, Si, P, and N was relatively low (Tables 9–12) because most runoff occurred before ice-off and did not mix with the main lake bodies where biological removal takes place (Bergmann and Welch 1985). In 1980 the retention of these same elements was higher because most inflow occurred after ice-out and mixed with the lakes, allowing removal. Also, because the volume of summer inflow was higher in 1980 than in 1981, the difference in *total* retention for 1980 versus 1981 was greater than the percentages indicate. For example, SO_4 had a mean retention of 19% in the four lakes in 1981 and 47% in 1980, but the mean absolute retention by the four lakes was $6.6\ kg \cdot ha^{-1}$ in 1981 and $49.4\ kg \cdot ha^{-1}$ in 1980, a greater than sevenfold difference (from Tables 9–12). The mean retention of Si was 82% in 1980 and 65% in 1981, but the absolute retention difference was over fourfold, $18.0\ kg \cdot ha^{-1}$ in 1980 and only $4.0\ kg \cdot ha^{-1}$ in 1981.

Silica retention was generally higher than P retention at Saqvaqjuac because Si loading occurred mostly after ice-out when it was mixed with the lake body and biologically removed, whereas relatively more P loading occurred before ice-out when inflowing water passed out the outflow and biological removal was less complete.

Contribution of Lake Ice to Internal Loading

Freezeout, the exclusion of dissolved substances from growing ice, was 97% efficient or better for major cations and anions (Table 16), whereas concentrations of TP in ice averaged 40% and TN 47% of the mean concentration in underlying water during the ice growth period. Nitrate (NO_3) concentrations ranged narrowly from 2.5 to 4.2 $\mu g \cdot L^{-1}$ in lake ice, however, even though the mean NO_3 concentrations in underlying water were 4.5 in Spring, 5.5 in Far, 55 in P & N, and

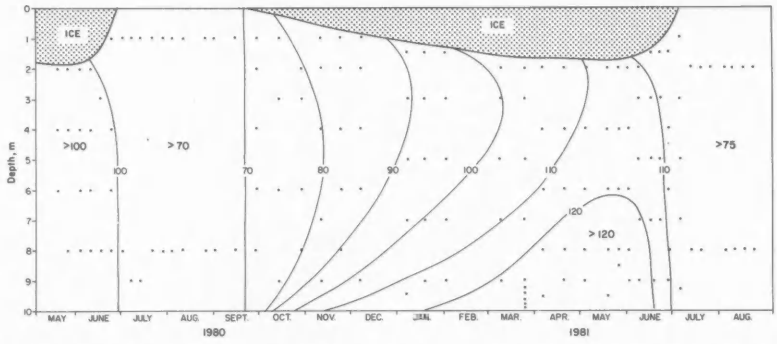

FIG. 10. Isopleths of specific conductance ($\mu S \cdot cm^{-1}$) in P & N Lake during the winter of 1980–81.

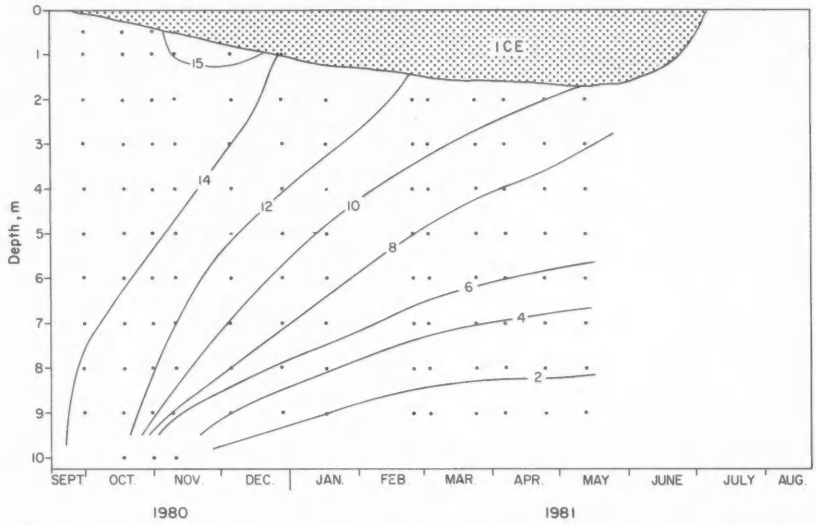

FIG. 11. Isopleths of oxygen concentration ($mg \cdot L^{-1}$) in P & N Lake during the winter of 1980–81.

223 $\mu g \cdot L^{-1}$ in Jade Lake (not shown), resulting in freezeout efficiencies of 98% down to 28% for NO_3 (Table 16). We presume that particulate and organic forms of N made up the differences. Since the source of P and N incorporated into lake ice was the lake itself, it was not a part of the external lake loading budget, but internally the release of P and N to a lake during icemelt was one fifth to over three quarters of the total annual P and N loading for these small headwater lakes (Table 17), even though it was probably not entirely available to biota in the underlying lake body (Bergmann and Welch 1985). The very high contribution of ice loading as a fraction of natural external loading for P & N Lake (Table 17) may have resulted from fertilization and the resultant incorporation of unnaturally high levels of P into the ice.

Investigators in the temperate zone have generally found even higher absolute amounts of P and N in black lake ice (Gröterud 1978; Adams et al. 1979; Barica and Armstrong 1971; Nakamoto et al. 1975), although periodic midwinter melts, the presence of slush, and high atmospheric loading make concentrations at midlatitudes difficult to interpret. The relatively high snow cover and P and N content of snow, and the relatively low volume of black ice, means the snow- and white ice-derived nutrient loading is more important than black-ice loading in temperate lakes (Adams et al. 1979; Barica and Armstrong 1971).

Distribution of Elements Beneath Lake Ice in Winter

In winter the distribution of most chemical species (Cl, Na, K, Ca, Mg, and SO_4) in small arctic lakes (this study; Schindler et al. 1974; H. E. Welch, pers. obs.) is similar. After freezeup, when lakes are completely mixed, freezeout increases solute concentrations beneath the ice, and this warmer, more saline water sinks and accumulates at the bottom (Welch and Bergmann 1985a) (Fig. 10). Total mass of these elements does not usually change over winter, showing that increased concentrations are a result of freezeout, not return from the sediment. Depth profiles show a peak concentration at the subice surface, a minimum of one-third maximum depth, and a second, higher peak at the bottom.

Oxygen isopleths show a different pattern because the sediments consume oxygen (Welch 1974; Welch and Bergmann 1985b), resulting in gradual depletion of oxygen in bottom waters (Fig. 11). Lakes with a mean depth >3 m usually have adequate oxygen to support fish overwinter, although Saqvaqjuac lakes as deep as 15 m maximum depth may have

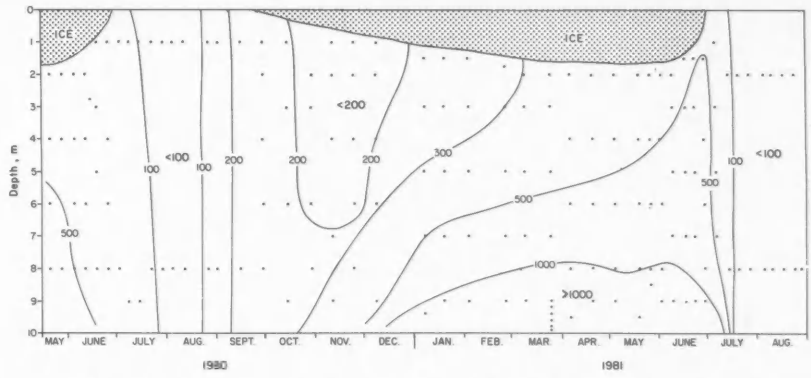

FIG. 12. Isopleths of Si concentration ($mg \cdot L^{-1}$) in P & N Lake during the winter of 1980–81.

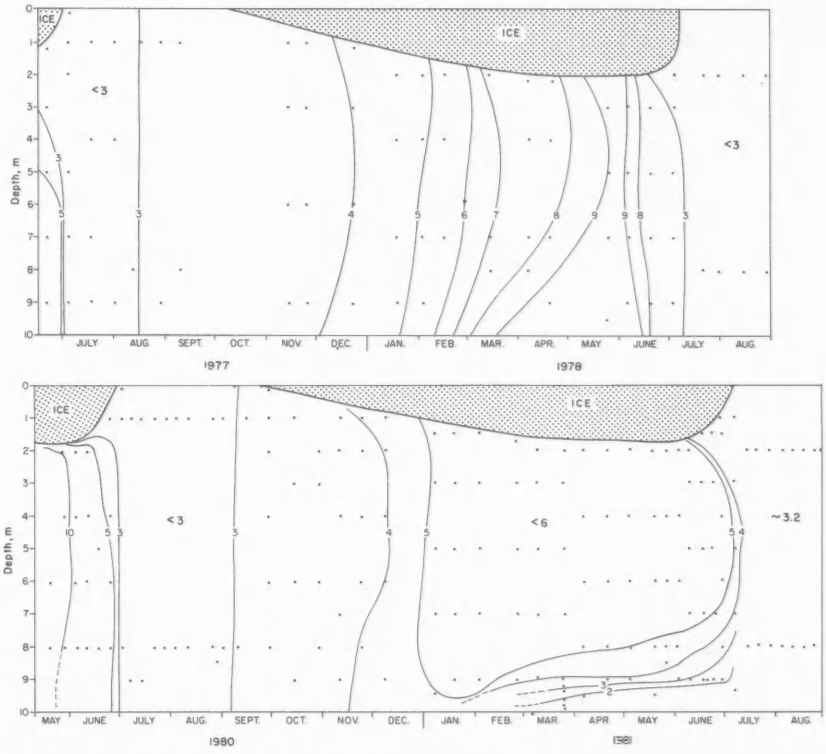

FIG. 13. Isopleths of SO_4 concentration ($mg \cdot L^{-1}$) in P & N Lake during the winter of 1977–78 (before fertilization) and 1980–81 (after fertilization.

a thin anaerobic layer of bottom water by March (H. E. Welch, pers. obs.). The bottom-most metre in P & N Lake was anaerobic in 1980–81 (Fig. 11), partly as a result of increased respiration due to fertilization with N and P (Welch and Bergmann 1985b).

Elements that return from the sediments into the overlying water have both freezeout and very high concentrations in the bottom water, as shown by Si (Fig. 12). There was very rapid depletion of Si in P & N Lake immediately after ice-out in 1981, presumably as a result of uptake by diatoms.

Sulphate concentrations and distribution in P & N Lake changed after fertilization (Fig. 13). Concentrations of SO_4 were distributed conservatively in 1977–78, whereas they were low in bottom water in 1980–81, coinciding with low bottom water O_2 concentrations (Fig. 13; and unpubl.). After eutrophication there was increased lake respiration and O_2 demand in P & N Lake (Welch and Bergmann 1985b), and SO_4 was probably being reduced in the bottom water in a matter analogous to SO_4 reduction in low-O_2 hypolimnetic waters at ELA (Kelly et al. 1982; Cook and Schindler 1984). The vertical circulation of lake water overwinter (Welch and Bergmann 1985a) suggests that sulfur may have undergone cyclic changes

TABLE 18. Change in element mass over winter. Slope and significance of regression of mass against time, September − June; $N \approx 11$ in 1977−78; $N \approx 16$ in 1980−81. NS = not significant ($p > 0.05$; *significant at $p < 0.05$; **significant at $p < 0.05$; ***significant at $p < 0.001$; ****significant at $p \leq 0.001$; sign of slope given as 0 where $p > 0.2$).

Element	P & N Lake 1977−78	P & N Lake 1980−81	Far Lake 1977−78	Far Lake 1980−81	Spring Lake, 1980−81	Jade Lake, 1980−81
Conductance	− (NS)	0 (NS)	+ (NS)	+ *	+ (NS)	0 (NS)
pH	+ *	+ *	0 (NS)	0 (NS)	0 (NS)	0 (NS)
Cl	− ****	0 (NS)	− *	0 (NS)	+ ***	0 (NS)
SO_4	+ ****	0 (NS)	+ ****	+ (NS)	− ****	0 (NS)
Na	0 (NS)	+ (NS)	0 (NS)	+ ****	+ ****	0 (NS)
K	− (NS)	+ (NS)	− (NS)	+ (NS)	+ ****	+ **
Ca	+ ***	0 (NS)	0 (NS)	+ *	0 (NS)	+ (NS)
Mg	− *	0 (NS)	− **	+ (NS)	+ (NS)	0 (NS)
TP[a]	—	− ****	—	0 (NS)	+ (NS)	− ****
TN[a]	+ (NS)	+ ****	+ (NS)	+ (NS)	0 (NS)	+ ****
Si	+ (NS)	+ ****	0 (NS)	+ (NS)	+ ****	+ ***

[a] Includes amount incorporated into ice.

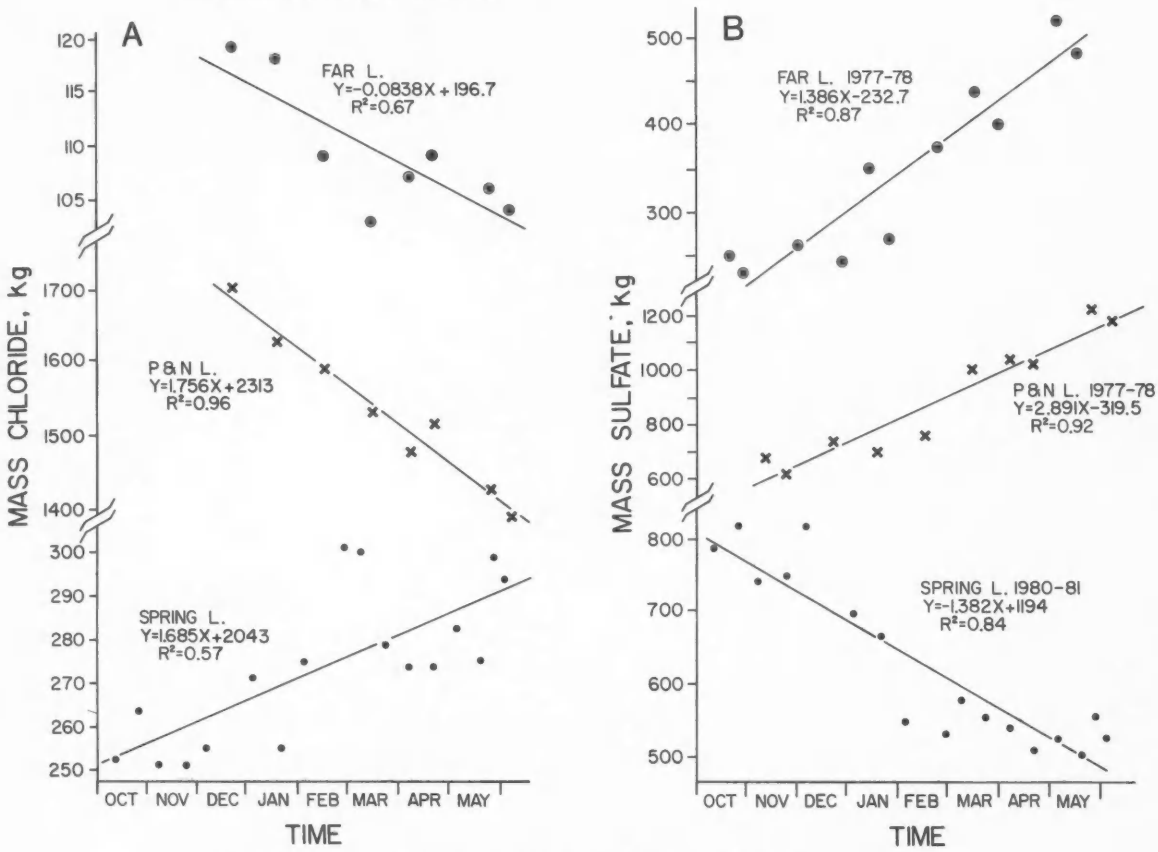

FIG. 14. Total mass of (A) SO_4 and (B) Cl in P & N, Far, and Spring lakes overwinter.

in oxidative state as it was transported, becoming reduced in the water adjacent to the sediments and oxidized higher in the water column.

Winter Mass Balance

Because the lakes were completely sealed by ice and permafrost from October to June, winter element mass balances reflected only internal lake processes. Element mass was regressed against time for each lake winter and the significance of the slopes calculated (Table 18) to determine whether elements were being lost or gained from the sediments overwinter. Conductance, pH, Mg, and Ca showed no strong trends. So-

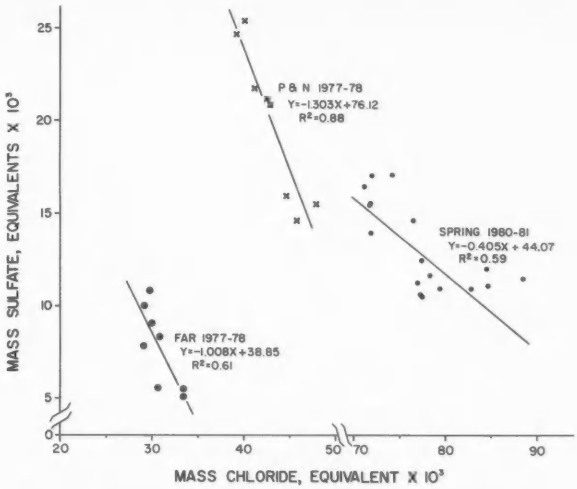

FIG. 15. Lake total equivalents of SO_4 plotted against total equivalents of Cl for P & N, Far, and Spring lakes overwinter.

dium and K returned from sediments in some lake years, notably Spring Lake. Total P and TN changed over winter only after fertilization in Jade and P & N lakes, which showed highly significant losses of P and return of N in 1980–81. Si tended to return in the most productive lake years but not in Far Lake, nor in P & N Lake before fertilization.

Chloride and SO_4 showed no significant trends in three lake winters, whereas in the other three lake winters there were strong trends (Table 18; Fig. 14). While SO_4 increased and Cl decreased in P & N and Far lakes in 1977–78, the opposite occurred in Spring Lake in 1980–81. Plots of equivalent masses for both ions (Fig. 15) show that in Far Lake, changes in one ion were exactly balanced by changes in the other (slope = −1.0); in P & N Lake, SO_4 increased slighly more than Cl decreased (slope = −1.3); and in Spring Lake, SO_4 decreased much less than Cl increased (slope = −0.4). We have no explanation for these results.

We attribute the significant returns of Cl, Na, and K overwinter in Spring Lake (Table 18) to the return of residual sea salt from the lake bottom, a result of the low elevation and recent uplift from marine inundation. Pagé et al. (1984) performed isotopic analyses on two meromictic lakes in the high arctic and concluded that meromixis had been caused by brine injection at depth as a result of permafrost encroachment and freezeout around the newly emerged lake basins. A similar process is probably occurring at Saqvaqjuac and could be causing the apparent flux of Cl, Na, and K into Spring Lake overwinter.

To our knowledge, only Schindler et al. (1974) have computed winter mass balances for polar lakes which undergo annual complete thawing. Their study showed that the mass of HCO_3, Ca, Mg, Na, Si, and probably K did not change overwinter in Char Lake. Chloride was apparently lost to the sediments.

In Fig. 16, the change in mass overwinter is plotted as a function of annual retention in Saqvaqjuac lakes. Conservative elements cluster around zero retention and zero winter change. As an element's retention increased, so did its return from the sediment overwinter. Phosphorus was the only element which was strongly retained *and* decreased in mass overwinter, and

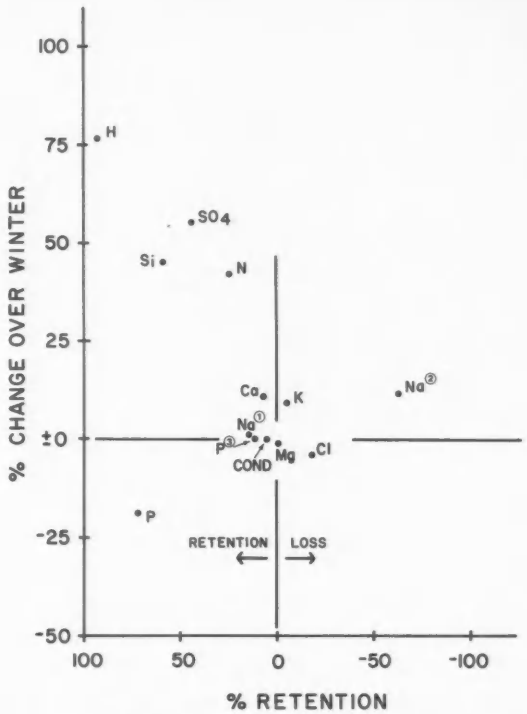

FIG. 16. Overwinter element mass balance plotted against annual retention for Saqvaqjuac lakes. 1 = P & N and Jade lakes, with added $NaNO_3$; 2 = Spring and Far lakes, no added $NaNO_3$; 3 = Spring Lake only (no added P); other P point is for Jade, Far, and P & N lakes.

that was only for fertilized lake years. Phosphorus in Spring Lake showed low retention and no change in winter mass. Sodium was surprising because under natural conditions (Far and Spring lakes) it had strong negative retention, whereas we expected it to fall inside the zero retention/zero winter change cluster.

Effects of Ice Cover on Solute Concentrations and Turnover Rates

Ice has two effects that increase the concentration of solutes of inflowing water. The first effect is freezeout, or cryoconcentration. For major ions, cryoconcentration (Table 16) is practically the same as the percent maximum ice volume of a given lake, or about 50–75% for Jade, Far, Spring, and P & N lakes. The second effect is the movement of dilute meltwater, both inflows and icemelt, through and out of a lake without mixing with the main lake body (Bergmann and Welch 1985). This effect increases the element renewal time compared with the theoretical renewal time, the discrepancy being greatest for lakes with low $A_D:A_0$, high $Z_{mean}:A_0$ or A_D, thick ice cover, and low summer rainfall relative to snowmelt runoff.

The net result of cryoconcentration and flow-through effects on solute concentrations is shown in Fig. 17. The lakes have about 60% more salt content than their inflows (the differences between the 1:1 diagonal and the eye-drawn data line). Evaporation (mean water retention, Table 14) is 12%. Evaporation therefore accounts for 12/60 = 20% of the concentration, with the remaining 80% resulting from the two ice effects mentioned

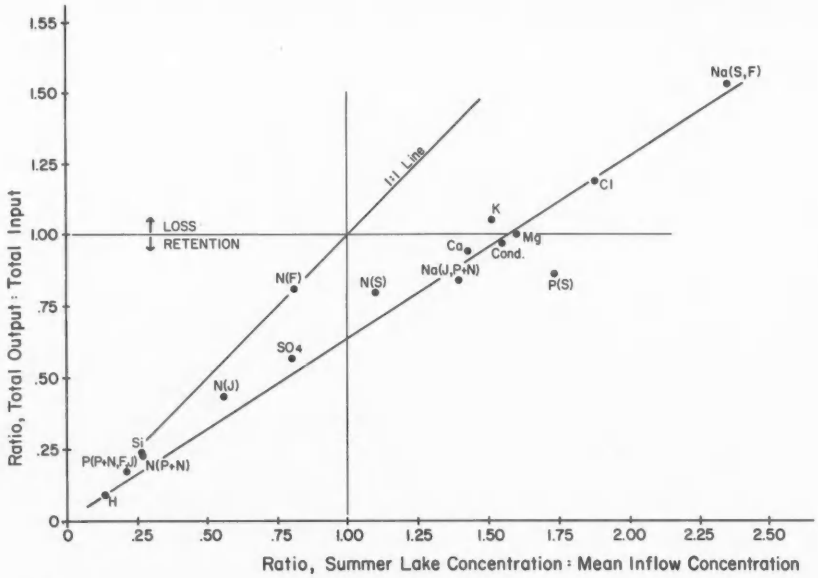

FIG. 17. Retention as a function of the ratio of summer lake concentration to mean inflow concentration for P & N, Far (F), Spring (S), and Jade (J) lakes. Note that the line drawn by eye crosses the zero retention line at ≈1.6.

TABLE 19. Turnover times for major ions and water in Saqvaqjuac lakes.

Lake	Year	Theoretical water turnover time (yr)[a]	Major element turnover time (yr)[b]					
			Cl	Na	K	Mg	Ca	$\bar{x}$
P & N	1978	2.6	—	—	—	—	—	—
	1979	5.5	8.8	7.8	7.1	7.0	6.2	7.4
	1980	2.5 } 2.9	2.7	2.7	3.1	2.7	3.4	2.9
	1981	3.5 }	6.0	7.4	6.4	7.2	8.1	7.0
Far	1978	2.6	—	—	—	—	—	—
	1979	5.1	—	6.1	5.6	5.0	5.4	5.5
	1980	1.8	2.1	2.5	1.8	1.9	2.0	2.1
	1981	2.2	3.4	3.8	3.0	3.6	3.6	3.5
Spring	1979	2.3	—	2.6	3.0	3.2	2.7	2.9
	1980	1.2	1.4	1.4	1.4	2.3	1.4	1.6
	1981	1.4	2.7	2.7	2.7	3.2	2.7	2.8
Jade	1980	0.8	1.6	1.6	0.8	1.4	1.4	1.4
	1981	0.9	2.9	3.6	—	4.3	4.8	3.9

[a]Lake volume − annual outflow.

[b]Turnover time = mass during open water season − annual mass outflow, for the dissolved fractions only. We have chosen to use outflow rather than inputs to calculate turnover times because we consider the outflow data to be more precise and accurate. Any dissolved input that sedimented to the lake bottom would reduce turnover rates. Tables 9−12 show that for these five elements, dissolved inputs ≈ dissolved outflow overall.

above. Low-latitude lakes with no ice should show only concentration differences due to evaporation, for conservative solutes.

In P & N Lake for 1980 and 1981 combined, the theoretical turnover time was 2.9 yr for water, whereas based on a whole-lake tritium-labelled water tracer experiment, the turnover time for the unfrozen water compartment was 3.5 yr (Bergmann and Welch 1985). The major ion turnover time for 1980−81 in P & N Lake actually averaged 4.1 yr (Table 19). Because 1980 and 1981 were so different in their summer water inputs, the assumptions made by Bergmann and Welch in order to combine the 1980 and 1981 experiment were undoubtedly not entirely correct; Table 19 suggests that the real discrepancy between theoretical and actual water renewal time for the sub-ice (unfrozen lake body) compartment was even larger than predicted. Table 19 shows that for 11 lake-years of data, major

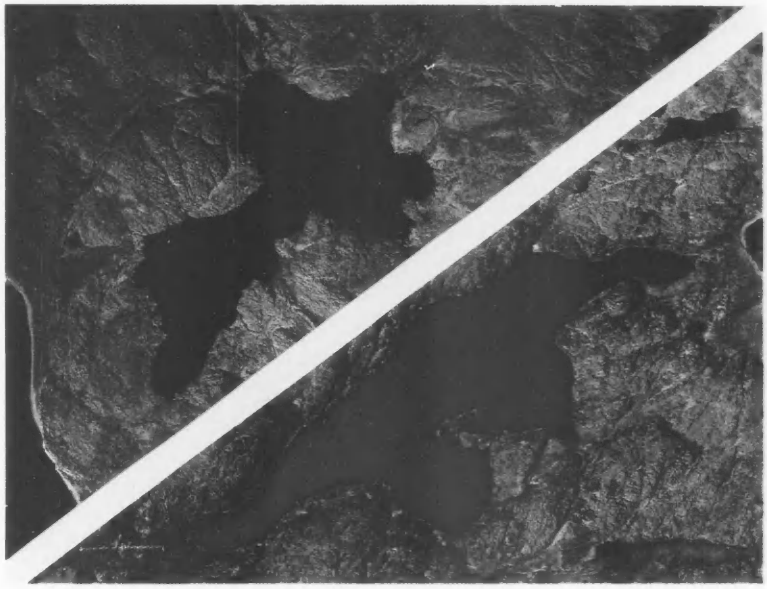

FIG. 18. Aerial photograph of Methane Lake (bottom) and Highway Lake (top), one of the three "green" lakes near the Saqvaqjuac Inlet which sustain permanent blooms of *Oscillatoria* and *Anabaena*.

TABLE 20. Saqvaqjuac lakes survey, 19 August 1978. A single surface sample was taken near the center of each lake.

Lake	Conductance ($\mu S \cdot cm^{-1}$)	Σ anions ($mEq \cdot m^{-3}$)	Σ cations ($mEq \cdot m^{-3}$)	$\frac{\Sigma \text{ anions}}{\Sigma \text{ cations}}$	Chlorophyll ($\mu g \cdot L^{-1}$)	Suspended carbon ($\mu g \cdot L^{-1}$)
"Dilute" lakes, mean	51.8	0.492	0.469	1.05	1.45	314
Range	24–105	0.288–0.937	0.280–0.941	—	0.52–3.48	200–570
N; SD	36; 20.9	29; 0.176	29; 0.190	—	28; 0.78	34; 99.6
No. 69 (Highway L.)	420	7.770	3.574	2.17	6.8	1200
No. 134 (Net L.)	200	1.687	1.757	0.96	4.8	1340
No. 37 (Hawk L.)	145	1.258	1.345	0.94	3.2	540
No. 83 (Green Tea L.)	360	2.948	3.091	0.95	—	1650
No. 74 (Spring L.)	115	1.147	1.209	0.95	1.4	300
Saqvaqjuac River	32	—	0.309	—	1.0	160

ion turnover times were always greater than theoretical water turnover times. This is a direct result, first, of cryoconcentration, and second, the subsequent maintenance of solute concentrations which are high relative to inflowing water, by the differential loss of low-density meltwater out the outflow.

Total P and TN, with their relatively high concentrations in lake ice (Table 16), behave differently. The loss of icemelt water through the outflow must mean that a large portion of P and N internal loading from icemelt is not made available to biota in the main lake body. Annual retention of P and N would probably be higher if freezeout was more efficient for these two nutrients.

Chemical Differences Between Lakes

On 19 August 1978, 41 lakes in the Saqvaqjuac area were surface-sampled by helicopter for major ion chemistry, one sample at the center of each lake. All but five lakes had less than 1 μEq cations or anions $\cdot L^{-1}$ and specific conductance less than 105 $\mu S \cdot cm^{-1}$ (Table 20). Mean Chl for the "dilute" lakes was 1.45 $mg \cdot L^{-1}$ and mean suspended C was 314 $\mu g \cdot L^{-1}$. The other five lakes had conductivities greater than 105 $\mu S \cdot cm^{-1}$ and solute concentrations greater than 2 $\mu Eq \cdot L^{-1}$ (Table 20). Three of the five lakes (Nos. 69, 93, and 134) had very high Chl and suspended C. All five are within several metres of sea level (Welch 1985; and pers. obs.). The Saqvaqjuac River, draining a 604-km^2 area with a maximum elevation greater than 140 m asl, had lower conductance than all but two lakes, and very low Chl and particulate C (Table 20). The lowest conductance (24 $\mu S \cdot cm^{-1}$) was found in Lake 151 at an approximate elevation of 50 m (not shown). There was, therefore, a strong trend of decreasing salt content with elevation which we cannot assess further because we lack precise elevation data.

Of the five high-solute lakes in Table 20, the three highest (Nos. 69, 93, and 134) also have high levels of Chl and suspended C. These three "green" lakes sustain permanent year-round high standing crops of filamentous blue-green algae (*Oscillatoria* and *Anabaena*; H. Kling, Freshwater Institute, Winnipeg, Man., pers. comm.), which is striking when seen from the air (Fig. 18). They did not visually change between 1976 and 1983, and they appeared to be in the same condition in a series of high-level black and white aerial photographs made in 1956. In addition to these "green" lakes adjacent to the Saqvaqjuac Inlet, we have noted several others within 100 km along the coast, always close to sea level.

The present coastal emergence rate is about 0.9 $m \cdot 100\ yr^{-1}$ for the Chesterfield Inlet area (Andrews 1969) which would make Spring Lake, about 3 m asl, only about 350 yr old. We suggest that recently emerged headwater lakes have high residual sea salt in their drainages which raises the salinity of the young lakes and increases the supply of P, currently about 35 $\mu g \cdot L^{-1}$ in Saqvaqjuac seawater during winter, resulting in the dominance of blue-green N-fixing algae. An analysis by Greg Brunskill (Freshwater Institute, pers. comm.) of sediment cores from Spring, P & N, Far, and Methane lakes has revealed the existence of a "transition zone" between the silty marine phase and the more recent organic lacustrine phase that has been described for lake sediment cores in the Kaminak Lake area of the south-central District of Keewatin, below the level of marine submergence (Shilts and Dean 1975; Shilts et al. 1976). We suggest that this "transition zone" was deposited when the lakes passed through the brief "green" phase shortly after emergence from the sea.

Trends in Lake Mass Balances

The 7-yr period for which we have data is not long enough to establish long-term trends. The essential micronutrients P, N, and Si changed annually in response to nutrient addition, and will be discussed elsewhere. Conductance, Na (in lakes without added $NaNO_3$), K, Mg, Ca, and pH showed no long-term trends (data not shown). However, the general increases in SO_4 content (Fig. 19), the generally high mean SO_4 retention of 43% (Table 14), and the decrease in Cl content of Saqvaqjuac lakes (Fig. 19) indicate that they were not in equilibrium for SO_4 and Cl during the study period.[2] Since Cl was decreasing but Na showed no trend, we conclude that the marine component of SO_4 loading was not increasing, and the marine component of atmospheric SO_4 loading was small anyhow (Table 5). Soil-derived SO_4 also probably did not increase, since Ca and Mg did not change. Increased loading from the atmosphere was a possible source of increased SO_4. The increased anthropogenic atmospheric SO_4 transport into the arctic (Barrie et al. 1981; Rahn 1984) might be expected to appear in lake mass balances.

We cannot explain the decrease in Cl levels in Saqvaqjuac lakes. Although the lakes are decreasing in salt content as the land rises from the sea, the decreases evident in Fig. 19 are much too rapid to be the result of uplift. Also, the major ion content of the same lakes did not change significantly during

[2] Analytical error does not seem to be the cause of either the long-term trends or the overwinter mass balances discussed previously. Since Cl and SO_4 were determined on the same sample, with Cl obtained by difference (Stainton et al. 1977), $Cl - SO_4$ can negatively covary on a sample-to-sample basis (unpubl.), but that could not cause covariance on successive sets of samples from different times or years.

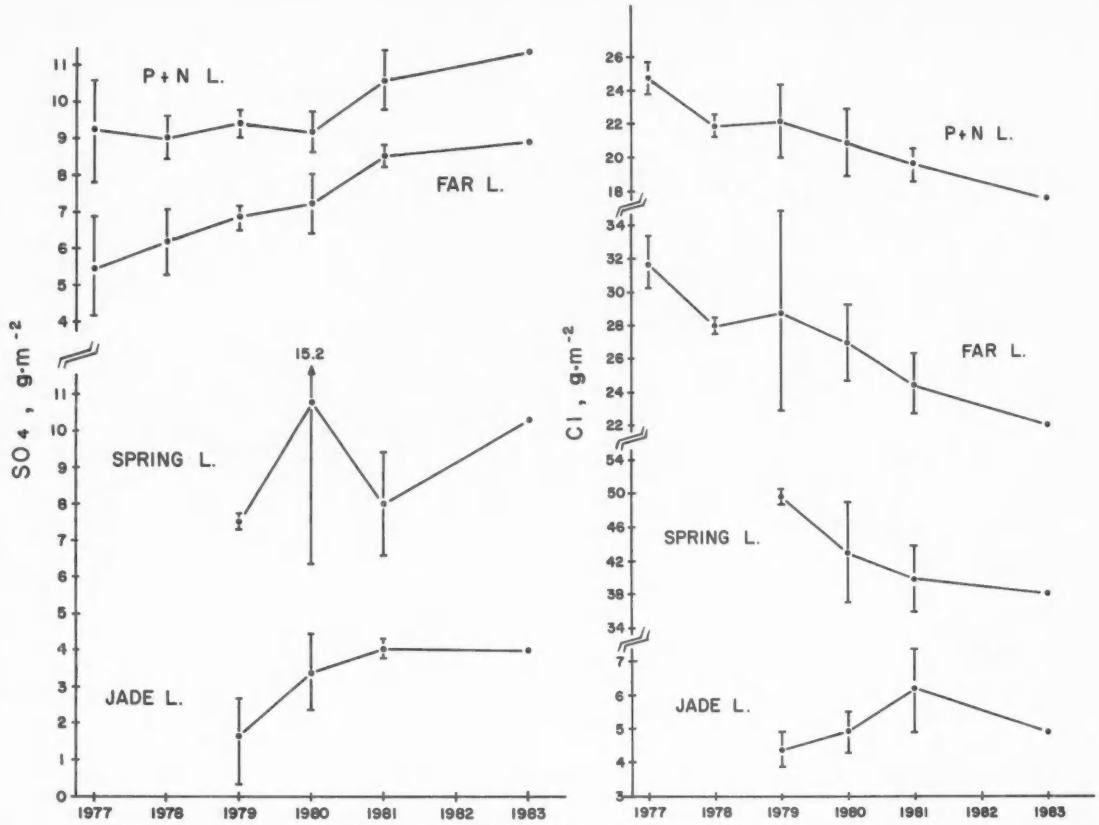

FIG. 19. Mean summer SO_4 and Cl content of Saqvaqjuac lakes (surface). There was only a single set of samples for 1983. Vertical bars are ± 2 SD.

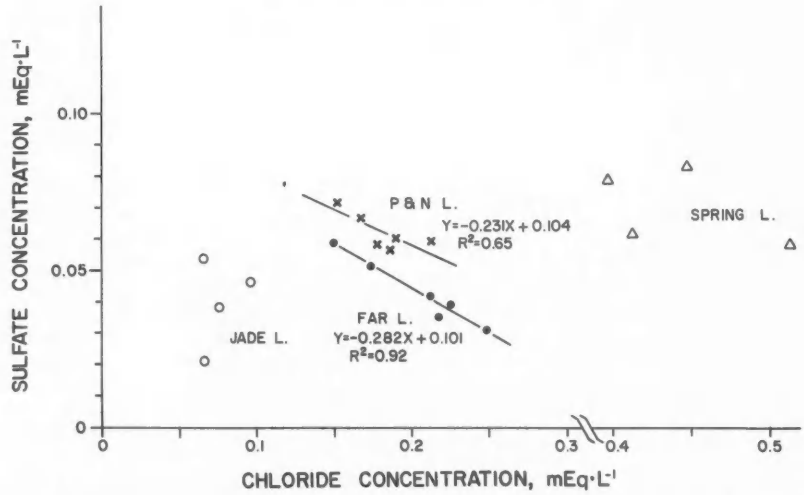

FIG. 20. Mean annual summer concentration of SO_4 plotted against Cl for P & N, Far, Spring, and Jade lakes.

the same time period (data not shown), and any change in salt balance as a result of uplift should have affected Na as well as Cl. We therefore suspect that changes in either Cl or SO_4 have resulted in corresponding changes in the other. On an equivalent basis, annual SO_4 changes were only about one fourth as much as Cl (regression slopes in Fig. 20), and may be anal-

ogous to Spring Lake Cl−SO_4 overwinter, where we presume that an increase in Cl resulted in a decrease in SO_4. On the other hand, overwinter data for P & N and Far lakes showed that SO_4 and Cl changed about evenly on a molar basis (regression slopes, Fig. 15). Schindler and Turner (1982) reported that artificial loading of H_2SO_4 to Lake 223 at ELA was accompanied by a 66% decrease in Cl.

Lakes serve as integrators of chemical loading on time scales ranging from months to many years, depending upon the water renewal rate. They may be sampled annually for far less cost than the maintenance of precipitation or stream sampling programs, especially in remote areas. We have therefore initiated a modest program to document long-term trends by sampling several lakes in the Saqvaqjuac, Yellowknife, and Resolute, N.W.T., areas annually for major ion concentrations.

Differences in Chemistry Between Arctic and Temperate Lakes

Arctic lakes are at one end of a continuum stretching from pole to pole, and as such are not different, in an absolute sense, from other lakes. The only unique feature that separates high-latitude lakes from lakes at lower latitudes is the presence of permafrost. Permafrost has little direct effect on a lake but profoundly alters the pattern of solute runoff from the lake's drainage, and may decrease the absolute amount of solute runoff as well by reducing the area of rock surface available for weathering. Thus, the loading of soil-derived elements such as Ca and Si may be greatly different from year to year, depending upon the seasonal pattern of runoff. Years with low late summer flows will have low output, whereas years with high late summer flows will have high output, much higher than the relative amounts of water discharge.

Although ice is not unique to the arctic, lake ice thickness and duration do increase with increasing latitude and altitude. Chemically, ice has two effects that tend to increase the concentration of dissolved solutes in lakes over that of inflowing water. The first effect is freezeout; the second is the movement of dilute meltwater through and out of a lake without mixing with the main lake body. These two effects are pronounced at Saqvaqjuac.

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References

ADAMS, W. P., M. C. ENGLISH, AND D. C. LASENBY. 1979. Snow and ice in the phosphorus budget of a lake in south central Ontario. Water Res. 13: 213−215.

ANDREWS, J. T. 1969. Present and postglacial rates of uplift for glaciated northern eastern North America derived from postglacial uplift curves. Can. J. Earth Sci. 7: 703−715.

BARICA, J., AND F. A. J. ARMSTRONG. 1971. Contribution by snow to the nutrient budget of some small northwest Ontario lakes. Limnol. Oceanogr. 16: 891−899.

BARRIE, L. A., AND J. M. HALES. 1985. The spatial distributions of precipitation acidity and major ion wet deposition in North America. Tellus.

BARRIE, L. A., R. M. HOFF, AND S. M. DAGGUPATY. 1981. The influence of mid-latitudinal pollution sources on haze in the Canadian Arctic. Atmos. Environ. 15: 1407−1419.

BERGMANN, M. A., AND H. E. WELCH. 1985. Spring meltwater mixing in small arctic lakes. Can. J. Fish. Aquat. Sci. 42: 1789−1798.

CHARLSON, R. J., AND H. RODHE. 1982. Factors controlling the acidity of natural rainwater. Nature (Lond.) 295: 137−140.

COGBILL, C. V., AND G. E. LIKENS. 1974. Acid precipitation in the northeastern United States. Water Resour. Res. 10: 1133−1137.

CONNORS, D. N., AND D. R. KESTER. 1974. Effect of major ion variations in the marine environment on the specific gravity−conductivity−chlorinity−salinity relationship. Mar. Chem. 2: 301−314.

COOK, R. B., AND D. W. SCHINDLER. 1984. Distributions of ferrous ion and sulfide in an anoxic hypolimnion. Can. J. Fish. Aquat. Sci. 41: 286−293.

DALTON, J. A. 1981. Hydrometeorological data from the Saqvaqjuac Project N.W.T., 1977 to 1980. Can. Data Rep. Fish. Aquat. Sci. 273: 43 p.

DE MARCH, L. 1975. Nutrient budgets for a high arctic lake (Char Lake, N.W.T.). Int. Assoc. Theor. Appl. Limnol. 19: 496−503.

DE MARCH, L., AND D. G. RUDY. 1978. Precipitation and water chemistry at Saqvaqjuac, N.W.T. (63°40′N, 90°40′W) 1977 data. Can. Fish. Mar. Serv. Data Rep. 104: 8 p.

GORHAM, E., F. B. MARTIN, AND J. T. LITZAU. 1984. Acid rain: ionic correlations in the eastern United States, 1980−1981. Science (Wash., DC.) 225: 407−409.

GRÖTERUD, O. 1978. Cryochemistry of lakes with special reference to formation, distribution and effect of phosphorus and hydronium. A preliminary report. Int. Assoc. Theor. Appl. Limnol. 20: 758−764.

JOHNSON, P. L., AND W. T. SWANK. 1973. Studies of cation budgets in the southern Appalachians on four experimental watersheds with contrasting vegetation. Ecology 54: 70−80.

JUNGE, C. E., AND R. T. WERBY. 1958. The concentration of chloride, sodium, potassium, calcium and sulfate in rain water over the United States. J. Meteorol. 15: 417−425.

KELLY, C. A., J. W. M. RUDD, R. B. COOK, AND D. W. SCHINDLER. 1982. The potential importance of bacterial processes in regulating rate of lake acidification. Limnol. Oceanogr. 27: 868−882.

KOERNER, R. M., AND D. FISHER. 1982. Acid snow in the Canadian High Arctic. Nature (Lond.) 295: 137−140.

LEWIS, W. M. JR., AND M. C. GRANT. 1979. Relationships between stream discharge and yield of dissolved substances from a Colorado mountain watershed. Soil Sci. 128: 353−363.

LIKENS, G. E., F. H. BORMANN, R. S. PIERCE, J. S. EATON, AND N. M. JOHNSON. 1977. Biogeochemistry of a forested ecosystem. Springer-Verlag, New York, NY. 146 p.

NAKAMOTO, N., M. OCHI-AI, T. MIZUTANI, AND H. HAYASHI. 1975. On the freezing-out properties of the lake ice. Jpn. J. Limnol. 36: 147−156.

PAGÉ, P., M. OUELLET, C. HILLAIRE-MARCEL, AND M. DICKMAN. 1984. Isotopic analyses (^{18}O, ^{13}C, ^{14}C) of two meromictic lakes in the Canadian arctic archipelago. Limnol. Oceanogr. 29: 564−573.

PERSSON, G., S. K. HOLMGREN, M. JANSSON, A. LUNDGREN, B. NYMAN, D. SOLANDER, AND C. ANELL. 1975. Phosphorus and nitrogen and the regulation of lake ecosystems: experimental approaches in subarctic Sweden, p. III-1 to III-19. *In* Proceedings of the circumpolar conference on northern ecology, September 15−18, 1975, Ottawa, Ont. National Research Council of Canada, Ottawa, Ont.

RAHN, K. A. 1984. Who's polluting the arctic? Nat. Hist. 93(5): 30−38.

RAHN, K. A., AND R. J. MCCAFFREY. 1980. On the origin and transport of the winter arctic aerosol. N.Y. Acad. Sci. Ann. 338: 486−503.

RIGLER, F. H. 1970. The Char Lake Project. A study of energy flow in a high Arctic lake, p. 278−300. *In* Z. Kajak and A. Hillbricht-Ilkowska [ed.] Productivity problems in freshwater. PWN, Warszawa.

SCHEIDER, W. A., W. R. SNYDER, AND B. CLARK. 1979. Deposition of nutrients and major ions by precipitation in south-central Ontario. Water Air Soil Pollut. 12: 171−185.

SCHINDLER, D. W., R. W. NEWBURY, K. F. BEATY, AND P. CAMPBELL. 1976. Natural water and chemical budgets for a small Precambrian lake basin in central Canada. J. Fish. Res. Board Can. 33: 2526−2543.

SCHINDLER, D. W., AND M. A. TURNER. 1982. Biological, chemical and physical responses of lakes to experimental acidification. Water Air Soil Pollut. 18: 259−271.

SCHINDLER, D. W., H. E. WELCH, J. KALFF, G. J. BRUNSKILL, AND N. KRITSCH. 1974. Physical and chemical limnology of Char Lake, Cornwallis Island (75°N. lat.). J. Fish. Res. Board Can. 31: 585−607.

SHILTS, W. W., AND W. E. DEAN. 1975. Permafrost features under arctic lakes. Can. J. Earth Sci. 12: 648–662.

SHILTS, W. W., W. E. DEAN, AND R. A. KLASSEN. 1976. Physical, chemical, and stratigraphic aspects of sedimentation in lake basins of the eastern Arctic Shield. Can. Geol. Surv. Can. Pap. 76-1A: 245–254.

SINGH, T., AND Y. P. KALRA. 1984. Predicting solute yields in the natural waters of a subalpine system in Alberta, Canada. Arct. Alp. Res. 16(2): 217–224.

STAINTON, M. P., M. J. CAPEL, AND F. A. J. ARMSTRONG. 1977. The chemical analysis of freshwater. 2nd ed. Can. Fish. Mar. Serv. Misc. Spec. Publ. 25: vi + 180 p.

VERRY, E. S. 1983. Precipitation chemistry at the Marcell Experimental Forest in north central Minnesota. Water Resour. Res. 19: 454–462.

WELCH, H. E. 1974. Metabolic rates of arctic lakes. Limnol. Oceanogr. 19: 65–73.

1985. Introduction to limnology at Saqvaqjuac N.W.T. Can. J. Fish. Aquat. Sci. 42: 494–505.

WELCH, H. E., AND M. A. BERGMANN. 1985a. Water circulation in small arctic lakes in winter. Can. J. Fish. Aquat. Sci. 42: 506–520.

1985b. Winter respiration in lakes at Saqvaqjuac, N.W.T. Can. J. Fish. Aquat. Sci. 42: 521–528.

WOO, M. K., AND R. HERON. 1981. Occurrence of ice layers at the base of high arctic snowpacks. Arct. Alp. Res. 13: 225–230.

WOO, M. K., R. HERON, AND P. MARSH. 1982. Basal ice in High Arctic snowpacks. Arct. Alp. Res. 14: 251–260.

Algal Competition for Phosphorus: The Influence of Zooplankton and Fish

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Interspecific competition for phosphorus between the blue-green alga *Anabaena flos-aquae* and the green alga *Staurastrum luetkemuelleri* was studied in enclosure experiments. Both algal populations increased in number upon introduction of fish, but addition of herbivorous zooplankton led to an increase solely in the *Staurastrum* population. This could not be attributed to grazing by zooplankton, chemical or physical conditions (light, pH, inorganic carbon), or the total supply or rate of supply of phosphorus. The observed differences were apparently due to the patchy release of phosphorus by the fish, and the more homogenous release of this nutrient by the zooplankton. This would allow the *Anabaena* species, which was capable of rapid uptake of temporary pulses of phosphate, to coexist with *Staurastrum* in the enclosures with fish.

On a étudié la compétition interspécifique pour le phosphore entre l'algue bleu-vert *Anabaena flos-aquae* et l'algue verte *Staurastrum luetkemuelleri* dans des expériences effectuées dans des enclos. Les deux populations d'algues se sont accrues à la suite de l'introduction de poissons, mais l'addition de zooplancton herbivore n'a conduit qu'à une augmentation de la population de *Staurastrum*. On n'a pu attribuer cela au broutage par le zooplancton, aux conditions chimiques ou physiques (lumière, pH, carbone inorganique) ou à l'apport total ou au taux d'approvisionnement de phosphore. Les différences observées étaient apparemment attribuables à la libération inégale de phosphore par les poissons et à la libération plus homogène de cette substance nutritive par le zooplancton. Cela permettrait à l'espèce d'*Anabaena*, qui était capable d'absorber rapidement des augmentations temporaires de phosphate, de coexister avec *Staurastrum* dans les enclos avec les poissons.

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Introduction of herbivorous zooplankton into enclosed communities of filamentous blue-green algae has resulted in collapse of the algal community (Stross 1973; Fott 1975; Andersson et al. 1978; Nyholm et al. 1978). Moreover, addition of fish, which rapidly remove the zooplankton, resulted in dense blooms of blue-green algae. Although even large filaments of some blue-green algae are partly ingested by large daphnids (Holm et al. 1983), it is not understood how the observed change in algal species composition could result solely from grazing. The object of our study was to investigate and explain this.

Materials and Methods

The field experiments were performed in Lake Haugatjern (Jacobsen 1974), situated in central Norway (63°29′N, 11°52′E, 697 m asl), from August 1979 to June 1980. In both years, two polyethylene bags (1.5 m diameter; 3.5 m deep) were stocked with zooplankton (ZOO-enclosures) and two with fish (FISH-enclosures) (see Table 1). The bags were suspended from the surface and anchored at 7 m depth in positions that ensured equal light regimes in all bags. They were open at the top and closed at the bottom, where loads were attached to ensure a vertical position. The initial phytoplankton biomass was 3–4 times higher in 1979 than in 1980 (Table 1), but the species composition was similar in both years. The colony-forming blue-green alga *Anabaena flos-aquae* and the desmid *Staurastrum luetkemuelleri* were the most abundant species. The cryptophyte *Rhodomonas lacustris* constituted less than 10% of the total biomass at the start of the experiments in both years.

All ZOO-enclosures except one (ZOO-1) were enriched with

TABLE 1. Initial biomasses (mg wet weight·L^{-1}) of phytoplankton, zooplankton, and fish in the enclosures. In 1979, the fish were yearlings of perch (*Perca fluviatilis*) and in 1980, 1-yr-old whitefish (*Coregonus lavaretus*).

Year		ZOO-1	ZOO-2	FISH-1	FISH-2
1979	Phytoplankton	8.6	8.0	7.7	10.7
	Zooplankton	2.0	6.6	0.2	1.2
	Fish	Excluded	Excluded	29	130
		ZOO-3	ZOO-4	FISH-3	FISH-4
1980	Phytoplankton	2.5	2.0	2.3	2.7
	Zooplankton	4.3	4.4	1.1	2.9
	Fish	Excluded	Excluded	96	256

zooplankton above the natural concentration, whereas ZOO-1 was run with the natural surface concentration of zooplankton. In a similar way, FISH-1 was stocked with about 800 kg fish·ha^{-1}, assumed to be representative for the lake. The remaining enclosures were operated at higher fish densities (see Table 1).

Integrated water samples (0–3 m) for chemical analyses and phytoplankton counting were taken with a tube sampler (length 1 m, volume 1.3 L). Zooplankton samples were taken as integrated water samples (0–3 m) with a modified Friedinger sampler (length 1 m, volume 5 L). A plankton net (mesh size 45 μm) was used to harvest the zooplankters.

Temperature and pH were measured in situ with a Montedoro–Whitney digital pH meter (model DPG-1B). Alkalinity was determined by titration with 0.01 mol HCl·L^{-1}. Insolation (400–700 nm) at the surface was measured continuously with a quantum sensor (LI-190 Lambda Instrument Corporation) and a Lambda LI-550 integrator, and the light transmission in the water was measured with a Lambda LI-185 and a quantum sensor LI-192 S. The samples for determination of dissolved total N, dissolved total P, PO_4-P, and NO_3-N were filtered through preignited Whatman GF/C filters and preserved with 0.02% HCl (N samples) or 4.5 mol H_2SO_4·L^{-1} (P samples). The concentration of orthophosphate and total dissolved P was determined according to Koroleff (1976a). Analyses of total dissolved N and nitrate were performed according to Koroleff (1976b) and Grasshoff (1976), respectively. Samples for determination of total particulate C and P were prefiltered through a 140-μm screen to remove the zooplankton, after which the samples were collected on Whatman GF/C filters and stored at −18°C until analysis. Particulate P was determined as orthophosphate after oxidation of the samples by UV radiation followed by boiling with HCl (three drops of concentrated HCl in 3 mL) in the presence of H_2O_2. Total particulate organic C was determined in a Carlo Erba CHN-analyzer (model 1104) after treatment of the samples with acidic fumes to remove carbonate. Samples for phytoplankton counting were preserved with Lugol solution and counted in an inverted microscope. *Anabaena flos-aquae* was counted in separate samples, which were sonicated to break up the colonies. The fresh weights of the algal samples were estimated by calculating their volume on a basis of geometric models and assuming a specific gravity of 1.0 mg·mm^{-3}. Primary production of the phytoplankton was measured by the ^{14}C method. Samples were incubated in situ for 4 h (10:00–14:00), and the radioactivity was determined in a liquid scintillation counter (Packard model 1450 Tricarb). Total inorganic C in the lake water was calculated from measurements of alkalinity and pH. Daily primary production was calculated by multiplying by a light factor (total daily insolation divided by insolation during the incubation period). The zooplankton samples were fixed with Lugol solution. The biomass was calculated according to Bottrell et al. (1976) and Langeland (1982) using length/weight regressions. The dry weight was assumed to be 10% of wet weight (Langeland 1982).

In the grazing experiments, lake water containing *A. flos-aquae* at 1–15 mg wet wt·L^{-1} was filtered through a 300-μm screen before it was transferred to 100-mL bottles. Known numbers of individuals of *Daphnia galeata* (2–21 individuals) were added to parallel bottles. The experiments also included control bottles without animals. All bottles were incubated in dim light at the ambient temperature (10–13°C) for 12 h before the experiment was terminated by adding Lugol solution. The number of colonies and fragments of *Anabaena* chains in the bottles were counted under an inverted microscope in sedimented samples.

Anabaena flos-aquae and *S. luetkemuelleri* were grown to steady state under P limitation in continuous cultures. The dilution rate was 0.1·d^{-1} and the illumination 90 μE·m^{-2}·s^{-1} (fluorescent light, Phillips tubes TL 40W-55 and TL 40W-33) in an 18 h light : 6 h dark regime. The temperature was 20°C and the phosphate concentration in the reservoir medium (Guillard and Lorenzen 1972) was kept at 5 μ*M*. The uptake rate of P was estimated by following the decrease of orthophosphate in cultures after injecting known quantities of orthophosphate. Before the start of the experiments, the cultures were diluted to a biomass of about 1–10 mg C·L^{-1}. The experiments lasted for about 15 min, and at least 10 samples were taken during this period. The algae removed 10–20% of the orthophosphate during the experiments.

Results

The concentrations of nitrate and orthophosphate remained at very low levels in the enclosures, whereas the concentration of total dissolved nutrients increased (Table 2). The pH remained rather constant, but a small increase was noticed in the FISH-enclosures as the experiment proceeded. In both years the total concentration of inorganic C remained constant in all bags. The light conditions of the enclosures are illustrated by the critical depth receiving 10% of the light intensity at the surface (Table 2). In both years the initial or critical depth was rather constant, although higher values were found in 1980. On day 9 the critical depth was lower throughout in the FISH-enclosures than in the ZOO-enclosures.

The algal biomass increased significantly ($P < 0.05$) in all enclosures except in the ZOO-1 bag which had the natural surface zooplankton density (Fig. 1; Table 3). The increase was most pronounced in 1980, when the initial phytoplankton biomass was low. The colony-forming *A. flos-aquae* and the large-sized desmid *S. luetkemuelleri* were the dominating algal species in the initial phase of the experiments, whereas the small cryptophyte *R. lacustris* occurred at lower densities (Fig. 2). The development in cell numbers for the different populations are shown in Table 3. A significant increase in the *Staurastrum* population ($P < 0.05$) was obtained in all enclosures except in the ZOO-1 bag. The cell density of *Anabaena* increased ($P < 0.05$) only in the enclosures with fish. The biomass of *Rhodomonas* decreased rapidly in all enclosures, except in the FISH-bags in 1979. The growth rates of the algae were higher

TABLE 2. Concentration of dissolved nutrients and total inorganic carbon (C_i) together with pH and the critical depth receiving 10% of the surface light intensity (D_{10}). Values for days 1 and 9 are given. The temperature was 11.6–14.4°C in 1979 and 15.5–15.8°C in 1980. n.m. = not measured.

Year	Bag	D_{10} (m)	C_i (mmol·L^{-1})	pH	Nitrate (μmol·L^{-1})	Orthophosphate (μmol·L^{-1})	Total N (μmol·L^{-1})	Total P (μmol·L^{-1})
1979	ZOO-1	2.0–2.4	0.64–0.65	9.3–9.2	<0.4–1.6	<0.03–0.03[a]	18.9–29.4	0.29–0.55
	ZOO-2	2.0–1.9	0.64–0.60	9.3–9.6	<0.4–0.4	<0.03–0.03	22.2–26.7	
	FISH-1	2.3–1.5	0.65–0.60	9.2–9.6	<0.4–0.4	<0.03–0.03	24.4–25.0	0.45–0.55
	FISH-2	2.0–1.0	0.64–0.60	9.3–9.6	<0.4–0.4	<0.03–0.03	18.9–25.6	0.36–0.58
1980	ZOO-3	3.2–2.5	0.61–0.61	9.5–9.5	0.6–0.4	0.1 –<0.03	n.m.	0.45–0.58
	ZOO-4	3.1–2.8	0.63–0.65	9.4–9.3	0.6–0.4	0.07–0.07	n.m.	0.39–0.65
	FISH-3	3.1–2.1	0.63–0.60	9.4–9.6	0.7–<0.4	0.07–<0.03	n.m.	0.32–0.55
	FISH-4	3.2–1.8	0.63–0.60	9.4–9.6	0.4–<0.4	0.10–<0.03	n.m.	0.42–0.52

[a]Detection limit was 0.03 μmol·L^{-1}.

TABLE 3. Apparent exponential increase rates of cell numbers (μ ± 95% C.I.) for the different algal populations and the total algal communities. Rates were obtained during periods of constant exponential growth if occurring or for days 1–9 of the experiments and estimated from linear regressions of $\log_2$ (cell volume) versus time (curves are shown in Fig. 1 and 2). n.a. = not available.

Enclosure	*A. flos-aquae*	*S. luetkemuelleri*	*R. lacustris*	Total Community
ZOO-1	−0.07±0.05[a]	−0.21±0.10[a]	n.a.	−0.08±0.06[a]
ZOO-2	0.01±0.02[a]	0.19±0.02	n.a.	0.04±0.02
ZOO-3	0.06±0.07[a]	0.45±0.06	n.a.	0.15±0.04
ZOO-4	−0.03±0.09[a]	0.48±0.08	n.a.	0.22±0.02
FISH-1	0.22±0.06	0.20±0.10[b]	0.47±0.07	0.19±0.04
FISH-2	0.25±0.12	0.24±0.03	0.54±0.02	0.22±0.04
FISH-3	0.25±0.13	0.27±0.03	−0.30±0.13[a]	0.20±0.09
FISH-4	0.30±0.04	0.35±0.12	n.a.	0.30±0.03

[a]*t*-test, $P(\mu > 0) < 0.95$.
[b]Obtained from days 5–15.

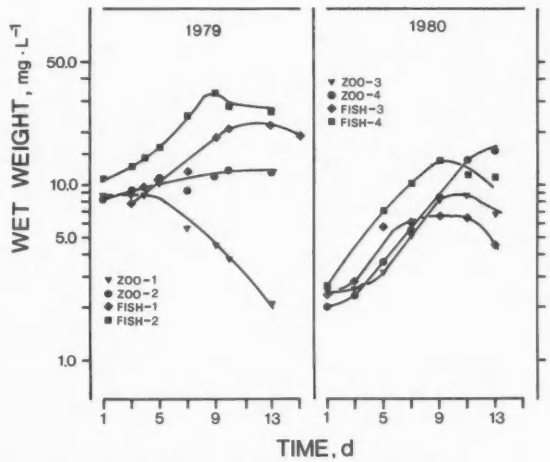

FIG. 1. Total biomass of phytoplankton in the different enclosures.

throughout in 1980 than in 1979.

In the ZOO-1 enclosure, no C assimilation occurred after day 5. Analysis of the data obtained from this enclosure is therefore restricted to the first 5 d of the experiment.

The P status of the algal populations indicated that P was the growth-limiting nutrient in Haugatjern and in the enclosure experiments (Olsen et al. 1983; Sakshaug et al. 1983). The highest mean P:C ratios (days 1–9, Table 4) were obtained throughout in the enclosures to which the highest biomass of fish or zooplankton had been added (see Table 1). The consumption rate of P for algal growth (U) is also given in Table 4 and was approximately the same in all bags except in the ZOO-1 and the FISH-4 enclosures (range 0.07–0.18 μmol P·L^{-1}·d^{-1}).

Short-term uptake rates of P for *S. luetkemuelleri* and *A. flos-aquae* grown under P limitation (Fig. 3) show that, at high concentrations, *Anabaena* could maintain considerably higher uptake rates of the element than could *Staurastrum*. The saturation level of the uptake rate was about 20 times higher in the former species. The half-saturation constants for uptake were 1.0 and 1.4 μmol P·L^{-1} for *Anabaena* and *Staurastrum*, respectively.

The total biomass of zooplankton (Fig. 4) was considerably higher in the ZOO-bags than in the FISH-bags. The larger animals (*Daphnia galeata*, *Diaptomus graciles*, and *Cyclops scutifer*) were rapidly removed from the water in the FISH-bags, whereas their biomass remained more or less constant in the ZOO-bags. In 1980, rotifers (i.e. *Polyarthra vulgaris* and *Keratella cochlearis*) constituted a significant fraction of the zooplankton at the start of the experiment. This group of animals decreased in biomass in the ZOO-bags, whereas they remained constant in the FISH-bags.

Daphnia galeata, with individuals ranging in size from 0.7 to 0.9 mm, was the most abundant zooplankton species in the

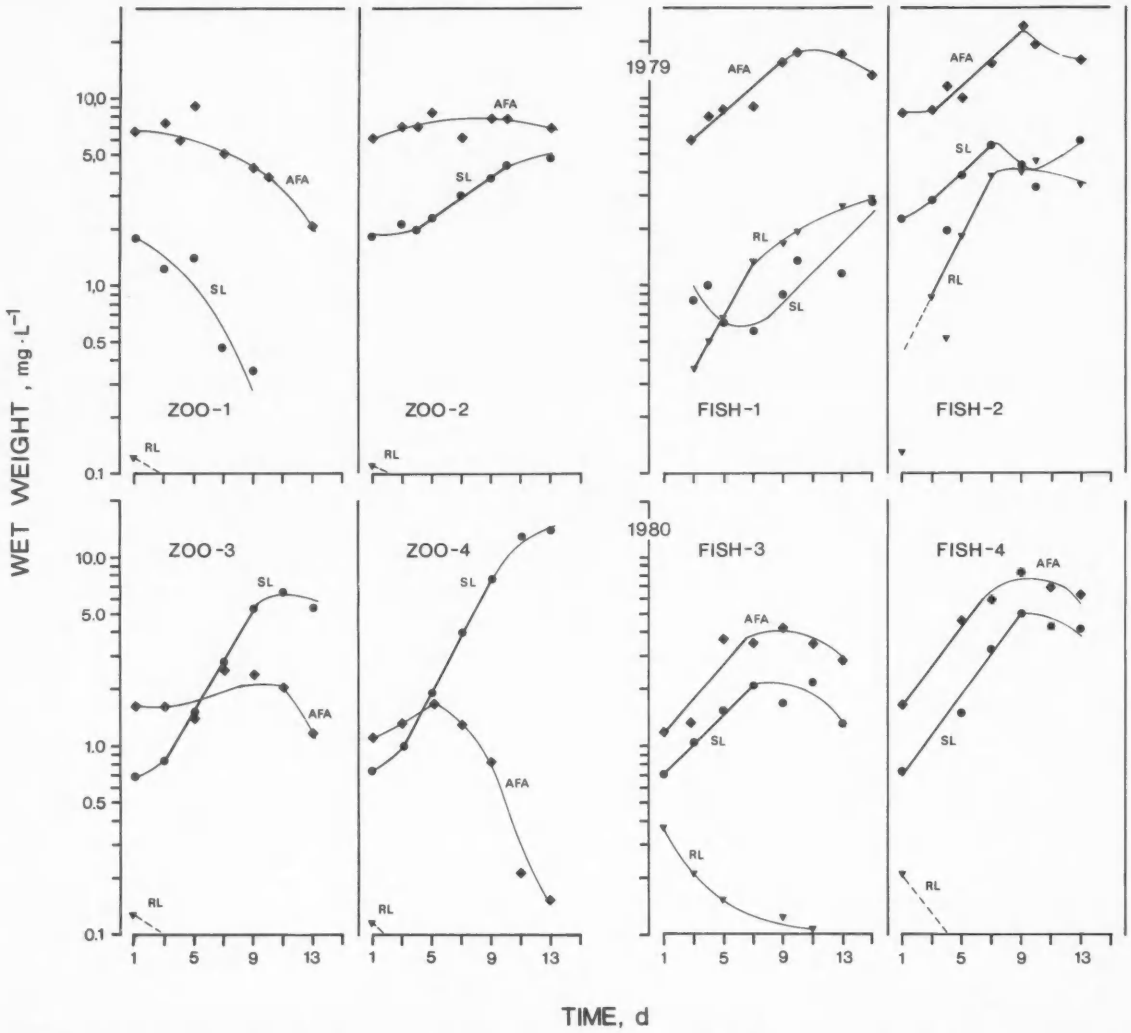

FIG. 2. Biomass development of the dominating algal species in the different enclosures. AFA = *Anabaena flos-aquae*, SL = *Staurastrum luetkemuelleri*, RL = *Rhodomonas lacustris*.

lake at the start of the experiments. Grazing rate measurements revealed that they were unable to consume *Anabaena* chains or coiled aggregates significantly (t-test, $P < 0.05$) unless the diameter of the colonies was less than 30–35 μm. This was also confirmed by microscopic studies of the behavior of the animals when feeding on colonies of *Anabaena*. All of the larger colonies were rejected by the animals.

The ability of the zooplankton to reduce the algal biomass is dependent upon their standing stock, their filtering rate, and their ability to ingest the different algal cells efficiently.

The maximum filtering rates of the present zooplankton communities were calculated from literature values: Cladocera (Geller 1975), Copepoda (Thompson et al. 1982), and Rotifera (Bogdan and Gilbert 1982). The results, given as litres filtered per litre of water and day (Table 5), represent potential upper limits to the algal mortality rates caused by grazing. This becomes equal to mortality if the animals feed at low concentrations, i.e. below the incipient limiting concentration (Geller 1975) of algae, and if the algae are efficiently ingested by the animals.

The results reveal higher filtering rates in the ZOO-enclosures than in the FISH-enclosures for each of the experimental years, indicating a higher grazing pressure in the former enclosures. In 1980, the FISH-enclosures were totally dominated by rotifers, which kept up a considerable grazing pressure, at least on smaller algae and similar food items. The contributions of the larger groups of zooplankton were, however, practically zero in all of the FISH-enclosures compared with those in the ZOO-enclosures.

Discussion

We observed a general pattern for the development of the algal species. Upon introduction of fish into the enclosures, all

TABLE 4. Mean P:C ratio of the algal cells and their P consumption rate for growth during the experiment (±1 SE). The consumption rate of P for growth is calculated as $P:C \cdot \Delta C$, where ΔC is the daily amount of C fixed by the algae.

	1979		1980	
	ZOO-1	ZOO-2	ZOO-3	ZOO-4
P:C ratio (10^{-3} atoms)	3.3±0.30	3.0±0.41	3.7±0.51	5.2±0.24
U(μmol $P \cdot L^{-1} \cdot d^{-1}$)	0.04±0.01	0.07±0.01	0.11±0.01	0.15±0.03
	FISH-1	FISH-2	FISH-3	FISH-4
P:C ratio (10^{-3} atoms)	3.7±0.23	4.3±0.31	6.0±0.72	8.25±1.17
U(μmol $P \cdot L^{-1} \cdot d^{-1}$)	0.09±0.01	0.18±0.02	0.16±0.03	0.42±0.08

TABLE 5. Mean calculated maximum filtering rates (d^{-1}) of the zooplankton in the initial phase (days 1–5) of the experiments. Ranges are given in parentheses. The estimates for *Cladocera*, *Copepoda*, and *Rotifera* are according to Geller (1975), Thompson et al. (1982), and Bogdan and Gilbert (1982), respectively. n.p. = not present.

Year		ZOO-1	ZOO-2	FISH-1	FISH-2
1979	Cladocera	0.12 (0.06–0.12)	0.89 (0.64–1.15)	0.01	0.04 (0.01–0.10)
	Copepoda	0.15 (0.07–0.25)	0.24 (0.16–0.37)	0.01	0.04 (0.01–0.08)
	Rotifera	n.p.	n.p.	n.p.	n.p.
	Total	0.27	1.13	0.02	0.08
		ZOO-3	ZOO-4	FISH-3	FISH-4
1980	Cladocera	0.35 (0.06–0.71)	0.45 (0.12–0.72)	0.01	0.01
	Copepoda	0.05 (0.03–0.09)	0.45 (0.12–0.72)	n.p.	n.p.
	Rotifera	2.33 (1.90–2.95)	1.49 (1.20–1.60)	0.69 (0.54–0.76)	1.02 (0.88–1.25)
	Total	2.73	2.10	0.70	1.03

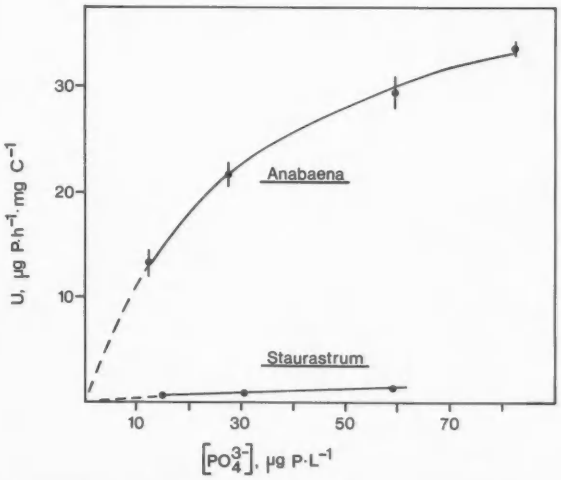

FIG. 3. Uptake rates of orthophosphate obtained for P-starved *A. flos-aquae* and *S. luetkemuelleri* grown at about $0.1 \cdot d^{-1}$. Bars indicate 1 SE of the measurement if visible.

dominating algal populations increased in biomass for a period of time, whereas only the *Staurastrum* species increased upon introduction of zooplankton. This was observed in both years, despite quite different initial experimental situations. There were few exceptions: in the ZOO-1 bag, none of the algal populations increased in biomass, and in 1980, *R. lacustris* was reduced in the FISH-bags, probably due to grazing by rotifers (see Table 5).

Grazing by zooplankton as well as supplementation of P and other changes in growth conditions may have been decisive for the development of the algal populations in the enclosures. The disappearance of *R. lacustris* from the ZOO-bags must be considered an effect of grazing because this species is a preferred food organism for the zooplankton (Reinertsen and Olsen 1984; filtering rates of Table 5). The decline in the *Anabaena* population was, however, not very likely an effect of grazing. The development of this species was different from that of *Rhodomonas*. It maintained a fairly constant biomass during the first part of the experiment, whereafter a rapid decrease was observed. The individuals of *D. galeata* were rather small (0.7–0.9 mm), and not able to ingest the colonies and aggregates of *Anabaena*. This has also been concluded by Porter and Orcutt (1980). Therefore, the observed development of *Anabaena* in the ZOO-bags, which was quite different from that in the FISH-bags, must be caused by factors other than grazing.

The initial physical and chemical conditions were more or less the same within each year. Some minor changes in pH and light conditions were noted at the end of the experiments, but these must have resulted from biological changes in the enclosures. Even if dense algal communities developed in some enclosures, and increases in pH were recorded, the concentration of inorganic C did not change significantly. The availability of inorganic C for algal growth is therefore regarded as equal for all enclosures.

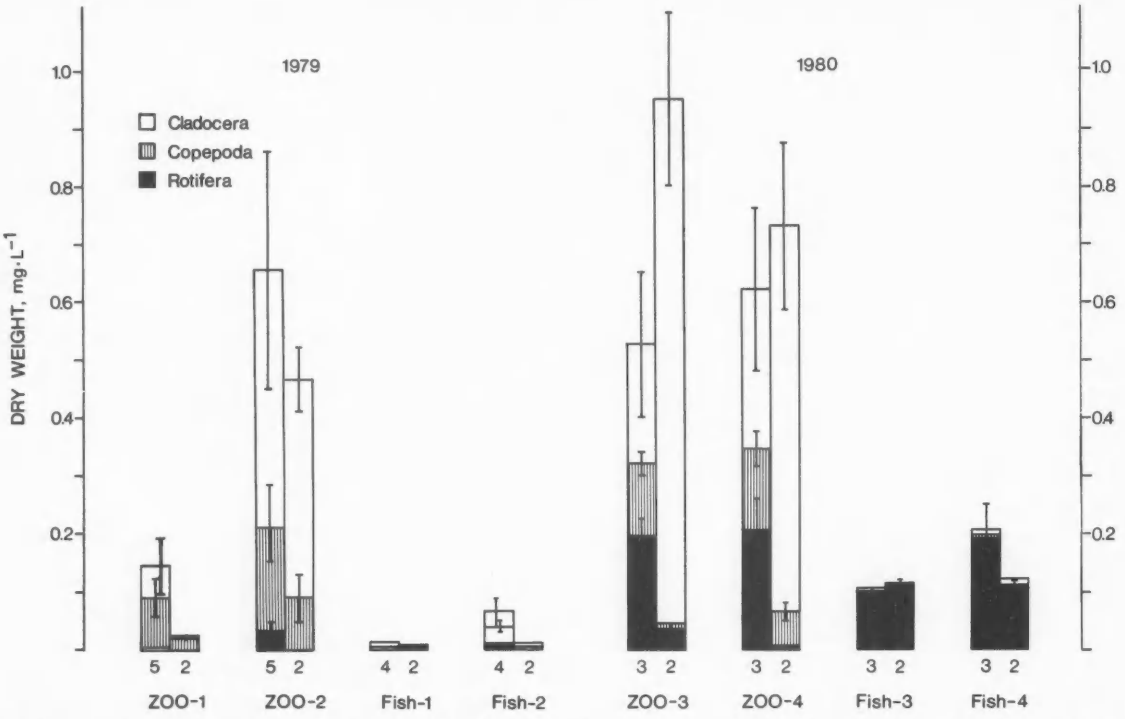

FIG. 4. Zooplankton biomass and composition at the initial (days 1–5) and the end phase (days 13–15) of the experiments. Bars indicate 1 SE and the numbers indicate number of samplings included.

Nitrogen was found to be in excess relative to P in the enclosures (Table 2). The latter element is therefore regarded as limiting for algal growth. This is supported by the relatively low P:C ratios obtained for the algae, and is in agreement with the conclusions of Olsen et al. (1983) and Sakshaug et al. (1983). Because the experiments were carried out in closed systems, extra P for algal growth could only come from the animals added to the enclosures, i.e. zooplankton or fish. If the algal consumption rates of P are taken as a measure of P supplementation from the animals, the results revealed that six out of eight enclosures received similar quantities of P during the experiment (days 1–9). The differences in species composition in the ZOO-bags relative to that of the FISH-bags can therefore not be explained as an effect of dissimilar P supplementation.

The total algal biomass was, however, related to the quantities of animals added, which must be expected in the closed systems used. Moreover, this explains the decline of the algal community in ZOO-1, which was supplied with far less P than was required for growth in the initial phase of the experiment.

Since neither grazing by zooplankton nor the quantities of P supplied can explain the species composition in the enclosures, it is necessary to examine the complexities of the system more closely. An important difference between the ZOO-bags and the FISH-bags was that the recycling of P was mediated by zooplankton in the former, whereas fish were an additional contributor in the latter. It is likely that fish release P in larger patches than those demonstrated for zooplankton (Jackson 1980; Lehman and Scavia 1982; Scavia and McFarland 1982) and that this was an important factor in the structuring of the phytoplankton community in the present experiments. The importance of the mode of nutrient supply upon the outcome of an algal resource competition has been emphasized by several workers (Grenney et al. 1973; Harris 1980; Tilman et al. 1982; Sakshaug and Olsen 1986; Sommer 1985). The ability of fish to supply short-lived pulses of P is fairly obvious and is supported by the following calculation. The concentration of P in living zooplankton is about 30 μg P·mg C^{-1} (Langeland et al. 1985). This corresponds to 1.5 g of P per litre of animals, assuming that C makes up 5% of the animals' fresh weight. If it is assumed that this concentration also applies to the feces of fish feeding on zooplankton, the concentration in feces is approximately 6–7 orders of magnitude higher than the average ambient concentration of reactive P in the lake water. Most of the P released by the fish is reactive (Lamarra 1975), and pronounced gradients of P in the surroundings of newly released feces or urine from fish must be expected (Jackson 1980). A heterogenous medium, in which the limiting nutrient occurs in patches rather than in a more homogenous pattern, favors algal species able to maintain high short-time uptake rates of P (Turpin and Harrison 1979; Sakshaug and Olsen 1986). Because *Anabaena* maintained considerably higher uptake rates of P when exposed to pulses of the nutrient than did the *Staurastrum* species (Fig. 4), it should either coexist with or outcompete *Staurastrum* in heterogenous systems.

Independent evidence in support of the above explanation was presented by Sakshaug and Olsen (1986). In competition experiments carried out in chemostat cultures, the present desmid *S. luetkemuellerii* was able to outcompete the blue-green alga *Microcystis aeruginosa* when phosphate was supplied con-

tinuously to the culture, whereas the latter species was superior if phosphate was supplied once each day as a pulse. These results support our conclusions even though another blue-green alga was involved. As demonstrated for the *Anabaena* species, *Microcystis* was also able to maintain a rapid uptake of phosphate when exposed to pulses of the nutrient.

Sommer (1985) has reported results in good agreement with those of Sakshaug and Olsen (1986) and our conclusion. In his competition experiments, no blue-green algae were able to establish in the chemostats supplied continuously with phosphate, whereas *A. flos-aquae* appeared in the pulsed cultures when the Si:P ratio was less than or equal to 40. However, it should be noted that these cultures were pulsed each week with 35 $\mu g\ P \cdot L^{-1}$ which caused a sevenfold increase of the total P concentration of the culture. Under such conditions, the species ability to accumulate large amounts of phosphate is probably more important than its capacity for rapid uptake.

The influence of zooplankton and fish on algal species development suggested above is not believed to apply only in bags. The important factors are different uptake characteristics of the algae and the different nutrient release pattern expected for animals of varying sizes. Both these factors are related to the organisms, and are therefore expected to be important in natural communities as well as in bags. We therefore conclude that dense fish stocks may favor the development of blue-green algae in lakes, and that the competitive advantage is reduced or lost when fish are removed or its density is greatly reduced and high densities of large herbivorous zooplankton are allowed to develop.

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References

ANDERSSON, G., H. BERGGREN, G. CRONBERG, AND C. GELIN. 1978. Effects of planktivorous and benthivorous fish on organisms and water chemistry in eutrophic lakes. Hydrobiologia 59: 9–15.

BOGDAN, K. G., AND J. J. GILBERT. 1982. Seasonal patterns of feeding by natural populations of *Keratella*, *Polyarthra*, and *Bosmina*: clearance rates, selectivities, and contributions to community grazing. Limnol. Oceanogr. 27: 918–934.

BOTTRELL, H. H., A. DUNCAN, Z. M. GLIWICZ, E. GRYGIEREK, A. HERZIG, A. HILLBRICHT-ILKOWSKA, H. KURASAWA, P. LARSSON, AND T. WEGLENSKA. 1976. A review of some problems in zooplankton production studies. Norw. J. Zool. 24: 419–456.

FOTT, J. 1975. Seasonal succession of phytoplankton in the fish pound Smyslov near Blatná, Czechoslovakia. Arch. Hydrobiol. Suppl. 46: 259–279.

GELLER, W. 1975. Die Nährungsaufnahme von *Daphnia pulex* in Abhängigkeit von der Futterkonzentration, der Temperatur, der Körpergrösse und dem Hungerzustand der Tiere. Arch. Hydrobiol. (Suppl.) 48: 47–107.

GRASSHOFF, K. 1976. Determination of nitrate, p. 137–145. *In* K. Grasshoff [ed.] Methods of seawater analysis. Verlag Chemie, Weinheim and New York.

GRENNEY, W. J., D. A. BELLA, AND C. C. HERBERG JR. 1973. A theoretical approach to interspecific competition in phytoplankton communities. Am. Nat. 107: 405–425.

GUILLARD, R. R. L., AND C. J. LORENZEN. 1972. Yellow–green algae with chlorophyllide *c*. J. Phycol. 8: 10–14.

HARRIS, G. P. 1980. Temporal and spatial scales in phytoplankton ecology. Mechanisms, methods, models, and management. Can. J. Fish. Aquat. Sci. 37: 877–900.

HOLM, N. P., G. G. GANF, AND J. SHAPIRO. 1983. Feeding and assimilation rates of *Daphnia pulex* fed *Aphanisomenon flos-aquae*. Limnol. Oceanogr. 28: 677–687.

JACKSON, G. A. 1980. Phytoplankton growth and zooplankton grazing in oligotrophic oceans. Nature (Lond.) 284: 439–441.

JACOBSEN, O. J. 1974. Feeding habits of the population of whitefish (*Coregonus lavaretus* (L.)) in Haugatjern — a eutrophic Norwegian lake. Norw. J. Zool. 22: 295–318.

KOROLEFF, F. 1976a. Determination of phosphorus, p. 117–126. *In* K. Grasshoff [ed.] Methods of seawater analysis. Verlag Chemie, Weinheim and New York.

1976b. Determination of total and organic nitrogen, p. 167–177. *In* K. Grasshoff [ed.] Methods of seawater analysis. Verlag Chemie, Weinheim and New York.

LAMARRA, V. A. 1975. Digestive activities of carp as a major contributor to the nutrient loading of lakes. Ver. Angew. Limnol. Verh. 19: 2461–2468.

LANGELAND, A. 1982. Interaction between zooplankton and fish in a fertilized lake. Holarct. Ecol. 5: 275–310.

LANGELAND, A., J. I. KOKSVIK, AND Y. OLSEN. 1985. Postembryonic development and growth rates of *Daphnia pulex* De Geer and *Daphnia galeata* Sars under natural food conditions. Int. Ver. Angew. Limnol. Verh. 22: 3124–3130.

LEHMAN, J. T., AND D. SCAVIA. 1982. Microscale patchiness of nutrients in plankton communities. Science (Wash., DC) 216: 729–730.

NYHOLM, N., P. E. SØRENSEN, K. OLRIK, AND S. D. PEDERSEN. 1978. Restoration of lake Nakskov Inderfjord, Denmark, using algal ponds to remove nutrients from inflowing river water. Prog. Water Technol. 10: 881–892.

OLSEN, Y., A. JENSEN, H. REINERTSEN, AND B. RUGSTAD. 1983. Comparison of different algal carbon estimates by use of the Droop-model for nutrient limited growth. J. Plankton Res. 5: 43–51.

PORTER, K. P., AND J. D. ORCUTT, JR. 1980. Nutritional adequacy, manageability, and toxicity as factors that determine the food quality of green and blue-green algae for *Daphnia*. Am. Soc. Limnol. Oceanogr. Spec. Symp. 3: 268–281.

REINERTSEN, H., AND Y. OLSEN. 1984. Effects of fish elimination on the phytoplankton community of a eutrophic lake. Int. Ver. Angew. Limnol. Verh. 22: 649–657.

SAKSHAUG, E., K. ANDRESEN, S. MYKLESTAD, AND Y. OLSEN. 1983. Nutrient status of phytoplankton communities in Norwegian waters (marine, brackish and fresh) as revealed by their chemical composition. J. Plankton Res. 5: 175–196.

SAKSHAUG, E., AND Y. OLSEN. 1986. Nutrient status of phytoplankton blooms in Norwegian waters and algal strategies for nutrient competition. Can. J. Fish. Aquat. Sci. 43: 389–396.

SCAVIA, D., AND M. J. MCFARLAND. 1982. Phosphorus release patterns and the effects of reproductive stage and ecdysis in *Daphnia magna*. Can. J. Fish. Aquat. Sci. 39: 1310–1314.

SOMMER, U. 1985. Comparison between steady state and non-steady state competition: experiments with natural phytoplankton. Limnol. Oceanogr. 30: 335–346.

STROSS, R. G. 1973. Zooplankton reproduction and water blooms, p. 467–478. *In* G. E. Glass [ed.] Bioassay techniques and environmental chemistry. Ann Arbor Science Publishers Inc., Ann Arbor, MI.

THOMPSON, J. M., A. J. D. FERGUSON, AND C. S. REYNOLDS. 1982. Natural filtration rates of zooplankton in a closed system: the derivation of a community grazing index. J. Plankton Res. 4: 545–560.

TILMAN, D., S. S. KILHAM, AND P. KILHAM. 1982. Phytoplankton community ecology: the role of limiting nutrients. Annu. Rev. Ecol. Syst. 13: 349–372.

TURPIN, D. H., AND P. J. HARRISON. 1979. Limiting nutrient patchiness and its role in phytoplankton ecology. J. Exp. Mar. Biol. Ecol. 39: 151–166.

Influence of Starvation and Subsequent Feeding on Body Composition and Energy Reserves in the Prawn *Pandalus platyceros*

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Biochemical composition of body segments and physiological condition of the spot prawn (*Pandalus platyceros*) were determined during 84 d of starvation and 21 d of subsequent feeding. Maximum molting frequency, 1.79%·d^{-1}, occurred from day 22 to 43 and mortalities peaked at 0.81%·d^{-1} on resumption of feeding. Ratios of wet weight of hepatopancreas to abdomen or whole body decreased on starvation and increased on feeding, and so provided an index of physiological condition. Uptake of moisture and chlorides with loss of other halides in prawn tissue resulted from starvation. Resting oxygen consumption rate declined by 50% after 40 d of starvation. Lipid in the hepatopancreas increased during early inanition to become the major energy source. Lipid contributed 73.1%, protein 20.6%, and carbohydrate 6.3% of total metabolized reserves. Hepatopancreas, carcass, and abdominal muscle generated 49.1, 33.4, and 17.5% of energy utilized. On subsequent feeding, lipid, carbohydrate, and protein accounted for 73.8, 20.1, and 6.1% of total caloric uptake with energy assimilation by body sections similar to depletion values. Spot prawn have sufficient reserves to remain in good commercial condition for 40 d without food.

On a déterminé la composition biochimique de parties du corps et l'état physiologique de la crevette tachée (*Pandalus platyceros*) pendant 84 jours de privation de nourriture suivis de 21 jours d'alimentation. La fréquence maximale de la mue, soit 1,79 %·j^{-1}, s'est produite entre le 22^{e} et le 43^{e} jour et les mortalités ont atteint un sommet à 0,81 %·j^{-1} à la reprise de l'alimentation. Le rapport entre le poids humide de l'hépatopancréas et de l'abdomen ou de tout le corps a diminué en période de privation de nourriture et augmenté en période d'alimentation, fournissant ainsi un indice de l'état physiologique. La privation de nourriture a amené l'absorption d'eau et de chlorures et une perte d'autres haloïdes dans les tissus des crevettes. Le taux de consommation d'oxygène au repos a diminué de 50 % après 40 jours de privation de nourriture. La teneur en lipides dans l'hépatopancréas a augmenté au début de la période de privation pour devenir la principale source d'énergie. Les lipides représentaient 73,1 %, les protéines 20,6 % et les hydrates de carbone 6,3 % de toutes les réserves métabolisées. L'hépatopancréas, la carcasse et le muscle abdominal ont produit 49,1, 33,4 et 17,5 % de l'énergie utilisée. Au cours de la période d'alimentation qui a suivi, les lipides, les hydrates de carbone et les protéines représentaient respectivement 73,8, 20,1 et 6,1 % des calories absorbées, l'assimilation d'énergie par les parties du corps étant semblable aux valeurs d'appauvrissement. La crevette tachée a suffisamment de réserves pour conserver une bonne qualité commerciale pendant 40 jours sans nourriture.

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Live holding of shellfish for retail sale is gaining acceptance as a means of quality assurance. Although environmental determinants have been established for the spot prawn *Pandalus platyceros* (Whyte and Carswell 1982), effects of prolonged holding under starvation conditions are unknown. This study was undertaken to assess these effects to provide a time frame for viable holding, to identify indicators of condition, and to detect changes in body composition and energy reserves, particularly those in the commercially important abdomen.

Conflict exists in the literature on the relative abundance and order of utilization of major energy reserves in decapod crustaceans. Major depletion of lipid reserves in the starved shore crab *Carcinus maenas* (Heath and Barnes 1970) contrasts with the predominant use of protein reserves in *Hemigrapsus nudus* (Neiland and Scheer 1953) and in the lobsters *Panulirus longipes* and *Nephrops norvegicus* (Dall 1974, 1981). Although lipid was considered the primary reserve of the crayfish *Orconectes nair* (Armitage et al. 1972), protein was metabolized predominantly in *O. virilis* (Hazlett et al. 1975) whereas both lipid and protein were used during progressive starvation of *O. limosus* (Speck and Urich 1969). The shrimp *Crangon crangon* starved for 4 wk consumed mainly carbohydrate, then lipid, and finally protein reserves (Cuzon and Ceccaldi 1972), yet from oxygen to nitrogen ratios of this starved species, lipid and protein were considered the principal sources of energy

(Regnault 1981). Composition of the hepatopancreas of the pink shrimp *Penaeus duoranum* starved for 12 d suggested initial use of lipid, then protein, and finally carbohydrate reserves (Schafer 1968). Biochemical changes in starved *P. japonicus* implied a reserve utilization of carbohydrate, lipid, and then protein (Cuzon et al. 1980). Yet another order of reserve utilization was indicated from biochemical changes in tissue sections of the tiger prawn *P. esculentus*, with protein from the abdomen considered the major source of energy and lipid of secondary importance (Barclay et al. 1983).

As well as reserve depletion during starvation, a decline in oxygen consumption was observed in starved *Carcinus maenas* (Klein Breteler 1975), *Crangon crangon* (Regnault 1981), and *Cancer pagurus* (Ansell 1973) yet no changes in metabolic rates were evident in starved *Panulirus japonicus* (Nimura and Inoue 1969) or in *Penaeus esculentus* (Barclay et al. 1983.)

These former studies of warmwater shrimp were conducted with starvation periods less than 30 d. In this study the cold-water *Pandalus platyceros* was starved 84 d and then fed for 21 d to identify definite trends in depletion and accumulation of energy reserves in sections of the body and to determine consequential effects on mortality, molting, and metabolic rates.

Materials and Methods

Prawns were trapped off Nanaimo, British Columbia, and transported in a self-contained live-holding tank to holding facilities at the Department of Fisheries and Oceans laboratory in West Vancouver, British Columbia. Holding tanks (700 L) were shaded and had a flow-through design providing 30 $L \cdot min^{-1}$ flow-rate of filtered (5 μm) constantly aerated seawater maintained at a depth of 1 m. Prawns were fed daily at satiation levels for 20 d with squid, herring, fresh beef liver, and fresh mussel in a sequential manner at a rate of approximately 0.5 $g \cdot d^{-1} \cdot prawn^{-1}$.

Conditions for Starvation/Feeding and Molt and Mortality Rates

Cylindrical holding cages (140 mm long, 62 mm diame. , 423 mL) were constructed from polyvinyl chloride rings and plastic screening. Male prawns (288, 26.0–34.4 mm carapace length), together with 1 g of mussel flesh, were positioned individually in the cages which were then stacked inside tanks (700 L) supplied with aerated filtered seawater. After 24 h, remaining food was removed and conditions of starvation maintained for a further 84 d. Thereafter a daily regime of feeding, as before, was undertaken for the next 21 d. Mean seawater temperature of 8.54°C (SD 0.48) and salinity 29.58‰ (SD 0.97) existed over the 105-d holding period. On days 0, 22, 43, 68, 84, and 105, specimens (35) at an intermolt stage were collected for chemical analyses. The percentage rate of molts between these collection days was calculated from $m \cdot (p\text{-}d)^{-1} \cdot t^{-1} \cdot 10^2$ where m represented molts between collection days, p was the population alive at the start of each holding period, d was recorded deaths, and t was the number of days during the holding period. Percentage mortalities per day was calculated from $d \cdot p^{-1} \cdot t^{-1} \cdot 10^2$.

Metabolic Rates

Prawns (26–29 mm carapace length, 12.5–19.1 g) positioned in cages were fed to repletion as mentioned previously. Oxygen consumption of fed animals was measured 24 h after removal of residual food from the cages to ensure that measurements represented postdigestive metabolism. Starved and fed animals (10 each) on days 0, 7, 27, 61, and 97 were placed in Erlenmeyer flasks (1 L) filled with seawater filtered to 0.22 μm.

Prawns were adapted to the flask for 1 h in air-saturated, filtered, running seawater (9°C, 29.6‰). Acclimation was always between 09:00 and 11:00 to avoid possible diel rhythms of respiration and excretion. Oxygen measurements by the method of Winkler (Strickland and Parsons 1968) provided metabolic rates calculated as mean microlitres per gram per hour with corresponding upper and lower confidence limits.

Sample Preparation

Prawns on days 0, 22, 43, 68, 84, and 105 were dried by blotting with paper, whole weight was recorded, and then cephalothorax and abdomen weights were recorded. The hepatopancreas was dissected from the cephalothorax and weighed, and the abdomen was freed from the shell and weighed. Abdominal exoskeleton was combined with remaining cephalothorax to be termed "carcass." Hepatopancreas and abdominal muscle were homogenized with twice their weight of water and the homogenate divided into two zip-lock bags and frozen at −40°C. Carcass was homogenized without addition of water. Content of 1 bag from each section of prawn was freeze-dried to provide percentage moisture.

Extraction of Lipid, Hydrophilic, and Polymeric Constituents

Extractive fractionation of prawn sections provided lipid, hydrophilic, and polymeric components (Whyte and Englar 1982). Frozen homogenized prawn tissue (50 g) weighed into a 400-mL beaker, with 185 mL of methanol and 92 mL of chloroform, was homogenized for 1 min. Following centrifugation at 12 000 rpm for 15 min, the centrifugate was removed and the residue reextracted with 250 mL of chloroform–methanol–water (2:4:1, v/v). This extraction was repeated twice and the combined extracts added to a 2-L separating funnel followed by 500 mL each of chloroform and water, and allowed to separate overnight at 1°C. The chloroform layer was removed, concentrated to an oil, and weighed as lipid. Evaporation of the aqueous methanol layer yielded a crystalline mass weighed as the hydrophilic fraction containing nonprotein nitrogenous and low molecular weight hydrophilic constituents. Residual material from extraction was suspended in water, frozen, freeze-dried, and weighed as the polymeric fraction containing polymeric carbohydrate and protein.

Chemical Parameters

Ash was determined by ignition of freeze-dried prawn sections (500 mg) in an electric muffle furnace at 550°C for 70 h and insoluble ash assessed by leaching ash contained in a 4.4-μm sinter Selas crucible with 100 mL of boiling water. Chloride and iodide were determined after alkali fusion of prawn tissue. An iodide selective electrode was used as the equivalence-point detector in argentometric titration for chloride, and as a differential potentiometer in the known-addition method for iodide (Whyte and Englar 1976, 1978). Similarly, fluoride was determined by the known-addition method using an Orion 94-09 fluoride selective electrode coupled to an Orion 90-01 single junction reference electrode as a differential

potentiometer. Plasticware was used throughout the analyses and the stock solution (100 mL) prepared by fusing 1 g of prawn tissue.

Nitrogen in the tissue and polymeric fraction was determined on 25 mg using micro-Kjeldahl techniques, with values from the latter multiplied by 6.25 to provide protein contents. Non-protein nitrogen from low molecular weight constituents in the hydrophilic fraction was estimated by difference. Total volatile nitrogen of abdomen and carcass was determined by acid titration of volatile bases in Conway diffusion cells (Conway 1957). Frozen diluted prawn tissue (30 g) in a Sorval Omni-mixer in an ice bath was homogenized for 2.5 min with trichloroacetic acid (1.4 g). The mixture, transferred to stainless-steel centrifuge tubes, was centrifuged at 11 000 rpm for 25 min at 5°C and the centrifugate analyzed immediately in a No. 1 Conway diffusion cell. The absorbing fluid (1.5 mL of 3.1% aqueous H_3BO_3 with 40-μL indicator of 0.033% bromocresol green and 0.066% methylred in ethanol), sealing fluid (1.5 mL of saturated aqueous Na_3PO_4 + KOH until turbid), and releasing fluid (1.5 mL as per sealing fluid) were positioned in appropriate chambers of the Conway cell and sample supernatant (1 mL) added to the releasing chamber. After 3 h of diffusion, back-titration of the absorbing fluid with 0.025 mol $HCl \cdot L^{-1}$ contained in a microburette provided micrograms nitrogen per millilitre.

Qualitative analysis of sugars was by gas-liquid chromatography. Acid hydrolysis of the polymeric and hydrophilic fractions (50 mg) with 0.5 mol $H_2SO_4 \cdot L^{-1}$ at 100°C for 16 h followed by neutralization with barium carbonate yielded parent sugars which were identified as corresponding alditol acetates (Sawardeker et al. 1965). Gas-liquid chromatography with meso-inositol acetate as internal standard used columns (1.8 m × 0.32 cm) of (a) 3% Silar 10C and (b) 3% Silar 5CP on Gas Chrom Q (100–120 mesh) operating at 205°C with a nitrogen flow rate of 30 $mL \cdot min^{-1}$.

Quantitative analysis of polymeric carbohydrate (glycogen) in the polymeric fraction and oligomers in the hydrophilic fraction used the phenol – sulfuric acid procedure (Dubois et al. 1956) and the alkaline–copper reagent (Horwitz 1975) with D-glucose as calibration sugar. Glycogen stock solutions were prepared by hydrolyzing 100 mg of dry polymeric fractions with 1 mol $H_2SO_4 \cdot L^{-1}$ at 100°C for 2 h and following filtration through Millipore glass-fiber, diluting the hydrolyzates to 100 mL for stock solutions. Glycogen values were obtained by multiplying equivalent glucose values by 0.90. Total carbohydrate in hydrophilic fractions was obtained by hydrolyzing 100 mg with 1 mol $H_2SO_4 \cdot L^{-1}$ at 100°C for 2 h. The hydrolyzate was filtered, neutralized to phenol red endpoint with 1 mol $NaOH \cdot L^{-1}$, and then diluted to 25 mL to give a stock solution for assessment by the alkaline–copper reagent.

Caloric content of lipid, protein, and carbohydrate in each prawn segment was calculated using factors 9.46, 4.32, and 4.18 $kcal \cdot g^{-1}$, respectively (Schafer 1968).

Results and Discussion

Replete male prawns were individually caged to prevent cannibalism during molting, although it was recognized that this suppression of activity might have an energy-conserving effect. Molting peaked from day 22 to 43 at 1.79% $\cdot d^{-1}$ but declined to zero as starvation progressed (Fig. 1). Resumption of molting at a rate of 0.18% $\cdot d^{-1}$ occurred on replenishment of energy by subsequent feeding. The highest frequency of mortality, 0.81% $\cdot d^{-1}$, also resulted from feeding, indicating the inability of some animals to recover from severe starvation. Approximately 55% of all mortalities occurred during or immediately after molting. Frequencies of molts (Fig. 1) suggested that animals starved for up to 43 d had energy reserves sufficient for normal physiological functions.

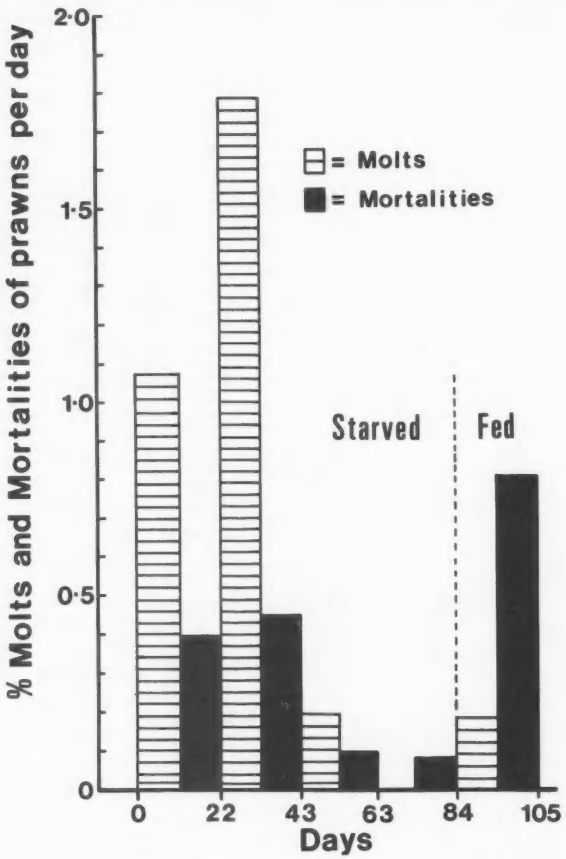

FIG. 1. Cumulative molt and mortality frequencies during periods of starvation and subsequent feeding of *P. platyceros*.

Prawns at an immediate pre- or post-molt stage (Schafer 1968) were not collected for physicochemical evaluation. Percentage of total fresh weight of different sections of the body changed as starvation progressed, with the increase in carcass following a decline in abdominal muscle and significantly the hepatopancreas (Table 1). Weight ratios of hepatopancreas to whole abdomen and to whole prawn declined nonlinearly with starvation time, yet both increased immediately on feeding to provide a measure of nutritional condition (Fig. 2). This index (Fig. 2a) applied to wild stock from Sarita and Coleman Creek in Barclay Sound, B.C., gave 0.086 and 0.092 for the 25–30 mm size class, respectively, and 0.082 and 0.084 for the 35–40 mm carapace length size class, respectively, indicating an improved physiological state of the animals from the latter location. These indices in a live-holding situation would provide an accurate measure of nutritional condition of the stock.

TABLE 1. Proportion, moisture, ash, and halides of body sections for starved, then fed, *P. platyceros*.

Parameters	Holding days (starved 0–84; fed 84–105)					
	0	22	43	63	84	105
Prawn sections (% wet wt.)						
Hepatopancreas	4.4	3.2	2.1	1.6	1.5	3.2
Abdominal muscle	37.2	35.9	35.8	34.4	32.8	34.1
Carcass	58.4	60.9	62.1	64.0	65.7	62.7
Moisture (%)						
Hepatopancreas	57.0	51.8	65.7	74.3	78.0	71.9
Abdominal muscle	76.6	77.5	79.1	79.2	79.9	79.6
Carcass	70.5	72.3	73.0	74.1	78.3	76.9
Ash total (% dry)						
Hepatopancreas	3.92	3.08	4.84	7.29	10.41	7.12
Abdominal muscle	6.65	6.71	6.78	7.09	7.62	7.32
Carcass	25.28	26.14	27.69	29.74	27.44	27.65
Ash insoluble (% dry)						
Hepatopancreas	0.80	0.84	2.13	4.36	3.33	1.35
Abdominal muscle	2.52	2.56	2.26	2.14	1.66	1.82
Carcass	17.86	17.27	19.16	18.61	16.20	16.82
Chloride (% dry)[a]						
Abdominal muscle	0.99	1.18	1.41	1.56	1.79	1.56
Carcass	2.13	2.67	2.92	3.27	4.62	4.18
Iodide (ppm dry)[a]						
Abdominal muscle	32.30	1.70	0.83	2.46	0.84	5.48
Carcass	38.80	32.70	25.90	15.30	10.60	28.00
Fluoride (ppm dry)[a]						
Abdominal muscle	9.16	4.14	6.96	3.80	2.78	4.24
Carcass	56.7	73.7	55.3	34.2	31.7	43.8

[a]Insufficient hepatopancreas for halide determinations.

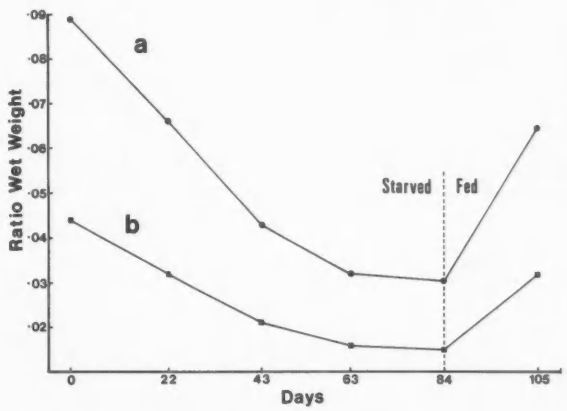

FIG. 2. Wet weight ratios of hepatopancreas to (a) whole abdomen and (b) whole body with time of starvation and subsequent feeding of *P. platyceros*.

Moisture uptake occurred in all segments of the prawn but most significantly in the hepatopancreas after 22 d of inanition. Accompanying this fluid uptake were soluble salts as judged from respective contents of total and insoluble ash (Table 1). Increase in content of chloride in abdomen and carcass suggested infusion of alkaline chlorides and loss of ionic control resulting from energy depletion. Ionic imbalance was also suggested by the rapid loss of iodide from the tail muscle over the first 22 d of starvation and the gradual loss of this anion from the carcass (Table 1). Similarly, fluoride levels associated with exoskeleton of crustaceans (Soevik and Braekkan 1979) decreased in the carcass as starvation progressed (Table 1). Reversal of ionic imbalance and trends in biochemical composition was effected by reenergizing the prawn on subsequent feeding, demonstrating the authenticity of observed changes on starvation (Table 1).

Lipid reserves in all segments of the prawn decreased with starvation except for an increase in the hepatopancreas during the first 22 d (Table 2). Corroboration of this increase, obtained by repeating the starvation with other prawns, suggested a mustering of lipid reserves in the digestive gland during early starvation as a conservation measure. Interestingly, an initial increase followed by decline in lipid composition was noted in starved *Balanus balanoides* (Barnes et al. 1963). The initial decline in polymeric and nonpolymeric carbohydrate in the digestive gland during this early period of starvation suggested that glycolysis and lipogenesis were active in augmenting this lipid reserve which proved to be the principal energy pool for the prawn (Table 2). Hydrolyzates of the polymeric fraction from hepatopancreas contained 2.4% galactose, 6.9% fucose, 8.2% mannose, 34.0% ribose, and 48.5% glucose whereas the

TABLE 2. Lipid, nitrogen, and carbohydrate components of body sections for starved, then fed, *P. platyceros*.

Parameters	Holding days (starved 0–84; fed 84–105)					
	0	22	43	63	84	105
Lipid (% dry)						
Hepatopancreas	45.6	61.0	41.6	32.1	18.0	24.7
Abdominal muscle	5.3	4.8	4.3	4.0	4.5	5.1
Carcass	4.6	4.1	3.5	3.0	3.2	4.0
Polymeric carbohydrate (% dry)						
Hepatopancreas	2.00	0.88	1.10	1.90	1.68	4.11
Abdominal muscle	0.34	0.40	0.37	0.33	0.33	0.42
Carcass	0.74	0.74	0.46	0.43	0.57	1.03
Nonpolymeric carbohydrate (% dry)						
Hepatopancreas	4.16	1.58	2.72	1.56	3.78	8.91
Abdominal muscle	0.79	0.79	0.79	0.64	0.61	1.10
Carcass	0.96	0.60	0.51	0.35	0.40	0.74
Protein nitrogen (% dry)						
Hepatopancreas	3.51	2.59	3.17	5.41	5.02	3.93
Abdominal muscle	11.06	10.79	10.67	11.09	10.56	9.93
Carcass	8.09	7.72	5.93	6.12	6.55	6.73
Nonprotein nitrogen (% dry)						
Hepatopancreas	1.74	1.83	2.67	2.96	4.26	3.86
Abdominal muscle	3.67	4.04	4.15	3.85	4.43	4.51
Carcass	0.35	1.10	2.26	1.48	1.01	1.26
Total volatile nitrogen ($\mu g\ N \cdot mL^{-1}$)						
Abdominal muscle	68.3	64.4	62.0	54.6	42.7	76.5
Carcass	110.0	75.3	85.1	75.6	77.4	67.2

hydrophilic fraction contained 1.3% inositol, 4.7% 2-deoxyglucose, 4.9% ribose, 11% mannose, 32.2% galactose, and 45.9% glucose, suggesting that glycogen and its depolymerisation products were principal carbohydrate reserves in the digestive gland. This differed from the carbohydrate composition of the abdominal muscle which contained 3.0% galactose, 14.4% mannose, 14.9% glucose, 27.7% ribose, and 50.0% 2-deoxyglucose in the polymeric fraction and 10.8% glucose and 89.2% ribose in the nonpolymeric, hydrophilic fraction of the muscle. During starvation, low levels of carbohydrates in the abdomen were stable and decreased only slightly in the carcass (Table 2).

Protein and nonprotein nitrogen in the hepatopancreas increased generally with starvation, but in the tail muscle and carcass, levels fluctuated and declined only slightly (Table 2). In contrast, results from starved *Penaeus esculentus* indicated that the largest contribution to energy metabolism was made by the protein of the abdomen which would affect the compositional quality of the muscle tissue (Barclay et al. 1983). Unlike the tiger prawn, therefore, the temperate-water spot prawn is capable of extended live-holding, without feeding, with only minimal effect on the composition of the commercial tail muscle.

At the micro level a decreasing content of total volatile nitrogen in the abdominal muscle became more acute after 43 d of starvation (Table 2), suggesting a decrease in protein catabolism and possible reduction in metabolic rate after this prolonged period of inanition. Resting oxygen consumption rates for another stock of starved and fed prawns over a 92-d period were in accord with this conclusion, demonstrating a

TABLE 3. Metabolic rates of *P. platyceros* under conditions of controlled feeding and starvation.

Days	Oxygen consumption ($\mu L \cdot g^{-1} \cdot h^{-1}$)			
	Fed prawns		Starved prawns	
	Mean	Confidence limits	Mean	Confidence limits
0	127	109–145	127	109–145
7	139	124–155	155	130–180
27	123	104–143	146	130–163
61	107	94–120	71	58–83
97	114	104–124	69	53–86

divergence of mean metabolic rates after 40 d of starvation (Table 3). These values were similar to the oxygen consumption rate for *Crangon vulgaris* ranging from 0.1 to 0.2 $mL \cdot g^{-1} \cdot h^{-1}$, which did not change with 8 d of starvation (Hagerman 1970). Resting oxygen consumption rate for *Penaeus esculentus*, 0.1 $mL \cdot g^{-1} \cdot h^{-1}$, again showed no detectable change over a 21-d starvation period (Barclay et al. 1983). However, *Crangon crangon* starved for 30 d, at a lower holding temperature of 12–14°C, showed a decrease in oxygen consumption rate from 0.15 to 0.06 $mL \cdot g^{-1} \cdot h^{-1}$ (Regnault 1981) in close agreement with values for the spot prawn (Table 3). A commercial holding period for spot prawn up to about 40 d was suggested from these metabolic rates.

Caloric content of partitioned prawns, calculated from absolute values of reserves, demonstrated energy contribution mainly from the lipid and protein of carcass and abdomen over

TABLE 4. Caloric content and rates of depletion/accumulation in sections of starved, then fed, *P. platyceros*.

Energy source (Reserves, cal · 100 g wet prawn^{-1}) (Rate, in parentheses, cal · 100 g^{-1} · d^{-1})	Holding days (starved 0–84; fed 84–105)					
	0	22	43	64	84	105
Hepatopancreas						
Lipid	8 143	8 901(+34)	2 834(−289)	1 249(−76)	562(−34)	2 081(+72)
Protein	286	172(−5)	99(−4)	96(0)	72(−1)	151(+4)
Total carbohydrate	295	175(−5)	114(−3)	84(−1)	82(0)	153(+3)
Reserves	8 724	9 248(+24)	3 047(−296)	1 429(−77)	716(−35)	2 382(+79)
Abdominal muscle						
Lipid	4 356	3 675(−31)	3 023(−31)	2 721(−14)	2 819(+5)	3 363(+26)
Protein	4 160	3 765(−18)	3 449(−15)	3 428(−1)	3 008(−21)	2 984(−1)
Total carbohydrate	411	402(0)	363(−2)	290(−4)	259(−2)	442(+9)
Reserves	8 927	7 842(−49)	6 835(−48)	6 439(−19)	6 086(−18)	6 789(+34)
Carcass						
Lipid	7 529	6 559(−44)	5 504(−50)	4 705(−38)	4 721(+1)	5 440(+34)
Protein	6 021	5 626(−18)	4 295(−63)	4 383(+4)	4 034(−18)	4 211(+8)
Total carbohydrate	1 224	945(−13)	680(−13)	541(−6)	578(+2)	1 072(+24)
Reserves	14 774	13 130(−75)	10 479(−126)	9 629(−40)	9 333(−15)	10 723(+66)
Total reserves	32 425	30 220(−100)	20 361(−470)	17 497(−136)	16 135(−68)	19 894(+179)

the first 22 d of inanition and then considerable energy production from the lipid of the hepatopancreas as starvation continued (Table 4). Of the total energy consumed (16 290 cal · 100 g^{-1}), 46.5% was derived from hepatopancreas lipid, 17.2% from carcass lipid, 12.2% from carcass protein, 9.4% from abdomen lipid, 7.1% from abdomen protein, 4% from carcass carbohydrate, 1.3% from hepatopancreas protein, 1.3% from hepatopancreas carbohydrate, and 1% from abdomen carbohydrate. Cumulatively the hepatopancreas contributed 49.1% of the total energy, the carcass 33.4%, and abdominal muscle 17.5%. Lipid provided 73.1% of total calories, protein 20.6%, and carbohydrate only 6.3%. Lipid in the hepatopancreas of *Penaeus duoranum* was also shown to be the primary source of energy (Schafer 1968) whereas the minor contribution to total energy of protein in *Pandalus platyceros* contrasted with the major metabolization of abdominal protein observed in *Penaeus esculentus* (Barclay et al. 1983). Carbohydrate contributed minimally as a source of energy in contrast to observations on starved *Crangon crangon* (Cuzon and Ceccaldi 1972) but contributed significantly to energy uptake on feeding, suggesting rapid interconversion to lipid akin to that observed in the digestive gland during the initial stages of starvation.

Energy accumulated in 21 d of subsequent feeding averaged 179 cal · 100 g^{-1} · d^{-1} which was lower than the energy loss over the previous 84 d of 194 cal · 100 g^{-1} · d^{-1}, but was considered to reflect the lag period in reserve assimilation which would follow severe starvation.

Storage of energy was partitioned as lipid in hepatopancreas, carcass, and abdomen at 40.3, 19.1, and 14.4%, respectively, as carbohydrate in carcass and abdomen at 13.1 and 5.0%, respectively, as protein in carcass and hepatopancreas at 5.0 and 2.1%, respectively, and as carbohydrate in hepatopancreas 2%. An overall negative energy balance for protein in the abdomen, −1%, suggested again its minimal role as a source of energy. Assimilation of energy in body segments as chemical reserves was similar to the order of utilization with hepatopancreas, carcass, and abdomen accumulating 44.4, 36.9, and 18.7% of total caloric energy. Lipid, carbohydrate, and protein accounted for 73.8, 20.1, and 6.1%, respectively, of total caloric uptake on feeding. The increased role of carbohydrate suggested its importance as an intermediate in interconversion of other reserves rather than as a primary source of maintenance energy.

In summary, the prawn *Pandalus platyceros* has a level of metabolic reserves sufficient for live-holding in a fasting condition for at least 40 d with only minimal mortalities. Even after extreme starvation for 84 d, prawns were capable of recovery on subsequent feeding. A reduction in oxygen consumption after 40 d of inanition agreed with a marked reduction in metabolic reserve utilization after this period. Order of contribution of metabolized reserves to energy requirements was lipid, protein, and then carbohydrate from hepatopancreas, carcass, and then abdominal muscle. Minimal compositional changes were evident in the latter commercial segment of the prawn. The ratio of wet weight of hepatopancreas to abdomen provided an index of nutritional condition of the prawn.

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References

ANSELL, A. D. 1973. Changes in oxygen consumption, heart rate and ventilation accompanying starvation in the decapod crustacean *Cancer pagurus*. Neth. J. Sea Res. 7: 455–475.

ARMITAGE, K. B., A. L. BUIKEMA, JR., AND N. J. WILLEMS. 1972. Organic constituents in the annual cycle of the crayfish *Orconectes nair* (Faxon). Comp. Biochem. Physiol. 41A: 825–842.

BARCLAY, M. C., W. DALL, AND D. M. SMITH. 1983. Changes in lipid and protein during starvation and the molting cycle in the tiger prawn, *Penaeus esculentus* Haswell. J. Exp. Mar. Biol. Ecol. 68: 229–244.

BARNES, H., M. BARNES, AND D. M. FINLAYSON. 1963. The metabolism during starvation of *Balanus balanoides*. J. Mar. Biol. Assoc. U.K. 43: 213–223.

CONWAY, E. J. 1957. Microdiffusion analysis and volumetric error. University Press, Glasgow. 465 p.

CUZON, G., C. CAHU, J. F. ALDRIN, J. L. MESSAGER, G. STEPHAN, AND M. MEVEL. 1980. Starvation effect on metabolism of *Penaeus japonicus*. Proc. World Maricult. Soc. 11: 410–423.

CUZON, G., AND H. J. CECCALDI. 1972. Influence de la stabulation a jeun sur le metabolisme de la crevette *Crangon crangon*. C. R. Seances Soc. Biol. (Marseille) 167: 66–69.

DALL, W. 1974. Indices of nutritional state in the western rock lobster, *Panuliris longipes* (Milne Edwards). I. Blood and tissue constituents and water content. J. Exp. Mar. Biol. Ecol. 16: 167–180.

1981. Lipid absorption and utilization in the Norwegian lobster, *Nephrops norvegicus* (L.). J. Exp. Mar. Biol. Ecol. 50: 33–45.

DUBOIS, M., K. A. GILLES, J. K. HAMILTON, P. A. REBERS, AND F. SMITH. 1956. Colorimetric method for the determination of sugars and related substances. Anal. Chem. 28: 350–356.

HAGERMAN, L. 1970. The oxygen consumption of *Crangon vulgaris* (Fabricius) in relation to salinity. Ophelia 7: 283–292.

HAZLETT, B., D. RUBENSTEIN, AND D. RITTSCHOF. 1975. Starvation, energy reserves, and aggression in the crayfish, *Orconectes virilis* (Hagen). Crustaceana (Leiden) 28: 11–16.

HEATH, J. R., AND H. BARNES. 1970. Some changes in biochemical composition with season and during the molting cycle of the common shore crab, *Carcinus maenas* (L.). J. Exp. Mar. Biol. Ecol. 5: 199–233.

HORWITZ, W. 1975. Glucose — chemical methods. Shaffer–Somogyi micro method. Official methods of analysis of the Assoc. Off. Anal. Chem. 12: 574–575.

KLEIN BRETELER, W. C. 1975. Oxygen consumption and respiratory levels of juvenile shore crabs, *Carcinus maenas*, in relation to weight and temperature. Neth. J. Sea Res. 9: 243–254.

NEILAND, K. A., AND B. T. SCHEER. 1953. The influence of fasting and of sinus gland removal on body composition of *Hemigrapsus nudus*. Physiol. Comp. Oecol. 3: 321–326.

NIMURA, Y., AND M. INOUE. 1969. Oxygen uptake rate of the Japanese spiny lobster as related to the environmental oxygen concentration. Bull. Jpn. Soc. Sci. Fish. 35: 852–861.

REGNAULT, M. 1981. Respiration and ammonia excretion of the shrimp *Crangon crangon* L.: metabolic response to prolonged starvation. J. Comp. Physiol. 141: 549–555.

SAWARDEKER, J. S., J. H. SLONEKER, AND A. JEANES. 1965. Quantitative determination of monosaccharides as their alditol acetates by gas liquid chromatography. Anal. Chem. 37: 1602–1604.

SCHAFER, H. J. 1968. Storage materials utilized by starved pink shrimp, *Penaeus duorarum* Burkenroad. FAO Fish. Rep. 57(2): 393–403.

SOEVIK, T., AND O. R. BRAEKKAN. 1979. Fluoride in Antarctic krill (*Euphausia superba*) and Atlantic krill (*Meganyctiphanes norvegica*). J. Fish. Res. Board Can. 36: 1414–1416.

SPECK, V., AND K. URICH. 1969. Consumption of body constituents during starvation in the crayfish, *Orconectes limosus*. Z. Vgl. Physiol. 63: 410–414.

STRICKLAND, J. D. H., AND T. R. PARSONS. 1968. A practical handbook of seawater analysis. Bull. Fish Res. Board Can. 167: 310 p.

WHYTE, J. N. C., AND B. L. CARSWELL. 1982. Determinants for live holding the spot prawn, *Pandalus platyceros* Brandt. Can. Tech. Rep. Fish. Aquat. Sci. 1129: 29 p.

WHYTE, J. N. C., AND J. R. ENGLAR. 1976. Determination of halogens in marine algae by use of an ion-selective electrode. Analyst 101: 815–819.

1978. Direct potentiometric measurement of chloride in fisheries products by ion-selective electrode analysis. J. Fish. Res. Board Can. 35: 202–207.

1982. Seasonal variation in the chemical composition and condition indices of Pacific oyster, *Crassostrea gigas*, grown in trays or on the sea bed. Can. J. Fish. Aquat. Sci. 39: 1084–1094.

Digestibility and Utilization of Canola Meal in Practical-Type Diets for Rainbow Trout (*Salmo gairdneri*)

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Hilton, J. W., and S. J. Slinger. 1986. Digestibility and utilization of canola meal in practical-type diets for rainbow trout (*Salmo gairdneri*). Can. J. Fish. Aquat. Sci. 43: 1149–1155.

The digestibility study indicated that dry matter digestibility of canola meal (CM) was low (56.2–60.4%), probably due to the high fiber content of this product and its relatively high level of complex carbohydrates. Energy and protein digestibility of CM were 72.4 and 83.2%, respectively, and the essential amino acid digestibilities were similar to those of protein in the CM. CM cannot successfully replace either soybean meal or fish meal in practical-type diets for young rainbow trout (*Salmo gairdneri*) without sacrificing growth. Supplementation with additional arginine, lysine and zinc, or energy to CM-based diets did not overcome the growth depressing effects. CM supplementation to the trout diet affected the thyroid gland of the fish, producing a diffuse, microfollicular hyperplasia that increased in severity with increasing CM supplementation. Young rainbow trout appear to be more sensitive to dietary glucosinolates than chinook salmon (*Oncorhynchus tshawytscha*), and total glucosinolate levels of 158 μg/g or more are deleterious to these fish. We conclude that CM should not, at this time, be included as a feed ingredient in commercial trout diets for young rainbow trout.

L'étude portant sur la digestibilité a montré que la digestibilité des matières sèches de la farine de canola (FC) était faible (56,2 à 60,4 %), en raison probablement de la teneur élevée en fibres de ce produit et de sa concentration relativement élevée en hydrates de carbone complexes. L'énergie et la digestibilité des protéines de la FC étaient de 72,4 et de 83,2 % respectivement, et la digestibilité des acides aminés essentiels était semblable à celle des protéines présentes dans la FC. La FC ne peut remplacer efficacement ni la farine de soya ni la farine de poisson dans les régimes alimentaires pratiques utilisés pour la jeune truite arc-en-ciel (*Salmo gairdneri*) sans sacrifier la croissance. L'addition d'un supplément d'arginine, de lysine et de zinc ou d'énergie aux régimes à base de FC n'a pas pallié les effets diminutifs sur la croissance. L'addition de la FC au régime alimentaire des truites a eu un effet sur leur glande thyroïde en provoquant une hyperplasie microfolliculaire diffuse qui s'est accentuée lorsqu'on augmentait la quantité additionnelle de FC. Les jeunes truites arc-en-ciel semblent être plus sensibles aux glucosinolates présents dans le régime alimentaire que les saumons quinnats (*Oncorhynchus tshawyscha*), et les concentrations de glucosinolates atteignant 158 μg/g ou plus sont nuisibles à ces poissons. Nous concluons que la FC ne doit pas, pour l'instant, être incluse comme ingrédient pour l'alimentation dans les régimes alimentaires commerciaux des truites pour ce qui est des jeunes truites arc-en-ciel.

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The complete replacement of fish meals with vegetable meals as the major protein source in fish diets results in a significant reduction in the growth and feed efficiency in the fish (Nose 1971; Cho et al. 1974; Koops et al. 1976; Hilton and Slinger 1981). The reasons for the relative inferiority of vegetable protein meals in fish diets are not completely understood.

Canola meal (CM) is the protein product produced from rapeseed low in erucic acid and glucosinolates (Canola Council of Canada, 1981). This vegetable protein meal has been used in salmonid diets with varying degrees of success. Yurkowski et al. (1978) found that CM could completely replace soybean meal and suggested that it could partially replace fish meal in rainbow trout (*Salmo gairdneri*) diets. Similarly, Hardy and Sullivan (1983) confirmed some of the observations of Yurkowski et al. (1978) in trout production diets; however, they suggested that future studies be conducted on young rainbow trout to determine the maximum safe level of CM incorporation. Similarly, studies on juvenile chinook salmon (*Oncorhynchus tshawytscha*) have also indicated that CM can supply some of the dietary protein and partially replace fish meal in salmonid diets (Higgs et al. 1982).

Recent research by Viola et al. (1982) on carp (*Cyprinus carpio*) has indicated that certain vegetable protein meals may have a reduced availability of energy and lysine to fish, which may account for the inability of vegetable meals to successfully replace fish meals. In addition, the high fiber content of vegetable protein sources can accelerate digesta passage through the intestinal tract (Hilton et al. 1983) which could reduce the digestibility of energy and protein. This may partially explain the observations of Viola et al. (1982). In addition, the increased fiber content could reduce the bioavailability of minerals, particularly zinc (Reinhold et al. 1975; Oberlas and Harland 1977). None of the previous studies on CM utilization in salmonid diets have included digestibility studies of the major organic nutrients and energy in this product.

TABLE 1. Formulation and analysis of the test diets (1–4) in experiments 1 and 2 (data represent percentages unless specified otherwise; ND = none detected).

Ingredient	Experiment 1				Experiment 2			
	1	2	3	4	1	2	3	4
Capelin meal (75.9% CP)	25	25	25	25	25	15	15	15
Soybean meal (51% CP)	30	20	10	—	25	25	25	25
Canola meal (36.7% CP)	—	13.5	26.9	40.4	—	35	35	36
Wheat middlings (18.6% CP)	26	23.5	20.5	17.8	35	7.5	5.5	1.5
Amino acid mix[a]	1	1	1	1	1	1	1	1
Amino acid mix[b]	—	—	—	—	—	—	1	—
Vitamin premix[c]	2	2	2	2	2	2	2	2
Mineral premix[c]	1	1	1	1	1	1	1	1
Zinc premix[d]	—	—	—	—	—	—	1	—
Fish oil (herring)	15	14	13.6	12.8	12	13.5	13.5	18.5
Analysis[e]								
Protein	40.8	40.4	39.7	38.9	39.1	39.7	41.0	38.6
Lipid	20.5	19.9	20.1	20.2	18.8	19.3	19.8	25.5
Ash	6.4	6.5	6.4	7.0	6.5	6.7	6.5	6.4
Zinc (mg/kg)	59.4	60.7	63.2	58.2	61.0	62.5	186.3	61.1
Glucosinolates (μg/g)[f]	ND	158	305	509	ND	441	441	418

[a]Supplied 0.4% DL-methionine and 0.1% L-arginine to the diets in experiment 1 and 0.4% DL-methionine and 0.2% L-arginine in experiment 2.
[b]Supplied 0.5% L-arginine and 0.5% L-lysine to the diet.
[c]As described in Hilton and Slinger (1981).
[d]Supplement 0.015% zinc as $Zn_2SO_4 \cdot 7H_2O$.
[e]Results based on the mean of three samples and expressed on a dry matter basis.
[f]Determined by the POS Pilot Plant Corp., Saskatoon, Saskatchewan.

We conducted this study to determine (1) the digestibility of the protein, essential amino acids, lipid, and energy components of CM to rainbow trout, (2) whether CM could replace soybean meal in practical-type diets fed to young rainbow trout, and (3) whether the supplementation of arginine, lysine and zinc, or increased energy in the form of lipid to CM-based diets increases the protein quality and/or utilization of this vegetable meal in practical-type diets for rainbow trout.

Materials and Methods

General Design

Canola meal (CM) was obtained from a commercial supplier (Canadian Vegetable Oils Inc., Burlington, Ontario) but the seed originated in western Canada. Samples were analysed for proximate composition by methods as described by Horwitz (1980), except for fat which was by the Bligh and Dyer method (1959). Two studies were then conducted to determine the digestibility and utilization of CM in rainbow trout. The first study was a digestibility experiment in which the feed, and resultant feces from the trout, were collected and analyzed for the apparent absorption of various nutrients. The second study consisted of two growth experiments in which CM was added to a practical-type trout diet as a replacement for either soybean meal (experiment 1) or a portion of the fish meal (experiment 2). The test diets in the digestibility study and those in both experiments 1 and 2 were analysed for ash, moisture, and protein content by the method of Horwitz (1980), lipid by the method of Bligh and Dyer (1959), and zinc by atomic absorption spectrophotometry as described by Lanno et al. (1985). The glucosinolate content of the test diets was determined after processing by the POS Pilot Plant Corporation, Saskatoon, Saskatchewan.

Digestibility Study

The digestibility study was conducted as described in Cho and Slinger (1979) with the exception that acid-insoluble ash (Atkinson et al. 1984) was utilized as the indicator instead of chromic oxide. Two diets were formulated: a reference and a test diet in which CM replaced 30% of the reference diet. The two diets were then fed to triplicate groups of rainbow trout, in two different aquatic systems, 3–4 times per day to satiety as described by Hilton and Slinger (1981). Both aquatic systems were thermostatically maintained at 15°C on a flow-through water supply system. The water supply was a 50:50 mixture of well water and dechlorinated City of Guelph municipal supply. The aquatic systems were housed in a windowless laboratory having a 12 h light : 12 h dark photoperiod. The first aquatic system used fish with an average weight of approximately 125 g (50 fish/tank), and feces were collected by the gravity feces collection technique (Guelph System) as described by Cho et al. (1982). The second system utilized fish averaging 45 g in weight (75 fish/tank), and feces were collected by the dissection or removal of the rectum as described in Hilton et al. (1982). The test diets and feces were analysed as previously described and the essential amino acid content of the diets and feces was determined after acid hydrolysis with 6 *M* HCl for 24 h and analysis on a Technicon amino acid ion exchange system with norleucine as an internal standard.

Formulation, Processing, and Analysis of Test Diets

In experiment 1 (replacement of soybean meal), four diets were formulated as described in Table 1 with CM replacing soybean meal on an isonitrogenous basis, at incremental levels from 0 to 40.4% of the diet. The diets were then steam pelleted on a laboratory pellet mill, dried in a fan-ventillated chamber at room temperature for 24 h, and stored at −5°C until required

for feeding. The test diets were then fed to quadruplicate groups of young rainbow trout (initial weight 2.0 g/fish) for 16 wk.

In experiment 2 (replacement of fish meal), one control diet and three test diets were formulated as described in Table 1, with CM replacing 10% of the original 25% fish meal incorporated into the test diet on an isonitrogenous basis. Diet 3 was supplemented with an additional 0.5% arginine and 0.5% lysine and 0.015% zinc in comparison with diet 2. Similarly, diet 4 was supplemented with an additional 5% fish oil in comparison with diet 2. The diets were then pelleted, dried, and stored as before. The test diets were fed to quadruplicate groups of young rainbow trout (initial weight 2.2 g/fish) for 16 wk.

Supply and Maintenance of Fish

Rainbow trout were obtained from a commercial trout farmer and acclimated to laboratory conditions for 4 wk prior to initiation of experiments 1 and 2. After the acclimation period, the fish were transferred to 32 circular, enamel-lined tanks (65 L) that were maintained on a biological filtration system with a fresh water replacement level of 5−15% per day. Water temperature was thermostatically maintained at 15.6 ± 0.7°C. Ammonia, dissolved oxygen, and pH were measured weekly in the aquatic system and varied from 0.0 to 1.5 mg/L, 7.0 to 8.5 mg/L, and 7.4 to 7.7 mg/L throughout the experiment. The tanks were housed in a windowless laboratory with a 12 h light : 12 h dark photoperiod. Quadruplicate groups of the trout (100 fish/tank) in experiments 1 and 2 were fed the test diets 3−6 times daily to satiety as described by Hilton and Slinger (1981).

Growth and Biochemical Analysis

The trout were weighed every 4-wk period and recounted and weighed at the end of 16 wk. Mortalities and feed consumption were noted daily and feed to gain ratios determined at the end of each period. At the end of 16 wk, six fish were sampled at random from each tank, anaesthetized with tricaine methanesulphonate (MS222, 200 mg/L, Syndel Laboratories) and blood sampled by caudal amputation for hemoglobin content (cyanmethomoglobin method) and hematocrit level using heparinized microhematocrit tubes. The fish were then killed by severing the spinal cord behind the head, individually weighed, and the liver removed. The livers were individually weighed, then frozen, freeze-dried, and analysed for zinc content by flame atomic absorption spectrophotometry as described by Lanno et al. (1985).

An additional 4 fish/tank were then sampled at random from each tank, anaesthetized with MS222, killed and ground with a meat grinder, frozen, and freeze-dried. The freeze-dried carcasses were then analysed for ash, lipid, moisture, and protein content as previously described. Similarly, the zinc content of the freeze-dried carcasses was also determined as previously described.

A further six fish were then sampled at random from each tank, anaesthetized with MS222, and blood collected in centrifuge tubes by amputation of the caudal peduncle. The blood was allowed to clot for at least 20 min and was then centrifuged for 5 min at 4000 × g. The serum was stored at −20°C until required for analysis. The serum was assayed for L-thyroxine (T_4) and triiodo-L-thyronine (T_3) content within 2 wk of collection. The serum T_3 and T_4 concentrations were determined using highly specific radioimmunoassay kits as described by Leatherland (1983).

TABLE 2. Dry matter, protein, lipid, energy, and essential amino acid (EAA) digestibility coefficients of canola meal in rainbow trout using the Guelph System (Cho et al. 1982) or rectum contents (Hilton et al. 1982) system of feces collection (data represent mean percentages of three samples on a dry matter basis; ND = not determined).

	Feces collection system	
Parameter	Guelph System	Rectum Contents
Dry matter	60.4	56.2
Protein	87.1	83.2
Lipid	92.5	91.8
Energy	75.4	72.4
EAA		
Threonine	90.5	89.1
Valine	78.6	77.4
Methionine	88.2	84.1
Isoleucine	80.0	80.3
Leucine	79.2	76.4
Phenylalanine	85.4	81.0
Lysine	87.2	81.2
Histidine	87.0	85.4
Arginine	86.4	83.6
Tryptophan	ND	ND

Histopathology

At the end of the 16-wk growth period, 10 fish were sampled from each of the groups in experiment 1 and groups 2 (diet 2) and 4 (diet 4) in experiment 2 for histopathological analysis (Aquatic Pathology Services, Guelph, Ontario). Specimens were killed with an overdose of MS222 and examined within 30 min. Necropsies were commenced at 11:00 and completed by 15:00 the same day.

Each fish was examined externally for any gross abnormalities, paying particular attention to the area around the ventral attachments of the gill arches. The entire isthmus, including the lower portions of the gill arches, was then excised and placed whole into 10% neutralized, buffered formalin. After at least 72 h of fixation, each tissue was trimmed, embedded in paraffin, sectioned at 6−7 μm, and stained with hematoxylin and eosin (H & E), according to standard procedures. All histological slides were first examined to determine the nature of the pathological changes; each histological section was qualitatively assessed as either normal or affected mildly, moderately, or severely. The entire group was then similarly assessed, according to the mean response based on these individual findings. When a group displayed the various pathological changes, each type of lesion category was assigned a value of either 1, 2, or 3 if the lesion was mildly, moderately, or severely advanced in the group, respectively.

Statistical Analysis

The results were subjected to analysis of variance and, where applicable, differences determined at the 5% level using Tukey's procedure as outlined by Steel and Torrie (1980). In addition, where applicable, the data were also subjected to linear regression analysis and tested with the F test for regression at the 5% probability level (Steel and Torrie 1980).

TABLE 3. Final body weight, feed to gain ratios, mortalities, and final carcass composition (mean of samples ± SD) of the trout after 16 wk at 15°C on the test diets in experiment 1 (canola meal replacement of soybean meal).

Parameter	Diet number (% canola meal) 1 (0)	2 (13.5)	3 (26.9)	4 (40.4)
Final body weight (g/fish)[a]	41.2±0.9	37.4±0.8	32.4±0.8	28.9±0.4
Feed:gain	1.0±0.1	1.0±0.0	1.1±0.0	1.1±0.0
Mortalities (%)	1.0±0.3	0.3±0.0	0.6±0.0	1.0±0.3
Carcass analysis[b]				
Protein	52.0	51.5	52.1	48.8
Lipid	40.2	41.0	40.4	43.4
Ash	5.9	5.8	5.8	5.6

[a]Initial weight 2.0 g/fish.
[b]Results expressed on a dry matter basis.

TABLE 4. Hemoglobin, hematocrit, serum thyroxine (T_4), serum triiodothyronine (T_3), liver to body weight ratio (LBW, (liver weight ÷ body weight) × 100), liver zinc, and carcass zinc content of the trout after 16 wk on the test diets (1−4) in experiments 1 and 2.

Parameter	Experiment 1 1	2	3	4	Experiment 2 1	2	3	4
Hemoglobin (g/dL)[a]	6.8±0.8	7.4±0.6	7.2±1.0	7.7±0.8	7.5±0.9	7.1±0.9	7.2±1.1	6.8±1.5
Hematocrit (%)[a]	35.8±2.9	39.4±4.2	37.3±3.5	39.3±3.6	37.3±4.2	37.1±3.7	37.5±4.0	37.6±5.0
LBW[a]	1.1±0.1	1.1±0.2	1.1±0.1	1.1±0.19	1.1±0.2	1.2±0.2	1.2±0.2	1.2±0.2
Serum T_3 (μg/dL)[b]	0.9±0.2	0.7±0.3	0.6±0.2	0.5±0.2	0.8±0.2	0.6±0.3	0.6±0.1	0.6±0.0
Serum T_4 (μg/dL)[b]	0.9±0.3	0.7±0.2	0.5±0.1	0.4±0.2	0.7±0.2	0.6±0.2	0.5±0.1	0.4±0.2
Liver zinc (μg/g dry weight)[b]	67.4±3.9	71.2±11.4	69.6±11.0	81.7±5.1	65.8±9.3	65.2±15.0	78.2±10.3	70.2±7.1
Carcass zinc (μg/g dry weight)[b]	23.0±5.4	22.3±2.9	29.1±2.9	34.7±2.1	28.0±6.2	21.4±1.4	52.1±5.7	22.9±1.4

[a]Results based on the mean of 6 fish per replicate ± SD.
[b]Results based on the mean of 8 fish per replicate ± SD.

Results

Digestibility Study

The two systems of feces collection gave slightly different results for the nutrient digestibility of CM (Table 2), with the Guelph system generally giving somewhat higher values. However, because the two feces collection techniques used different groups and sizes of fish, the results of the two techniques were not truly comparable and therefore were not subjected to statistical analysis. The CM had a percent dry matter digestibility of 56.2−60.4 and a protein digestibility of 83.2−87.1. The digestibilities of the essential amino acids (EAA) were somewhat similar to the digestibility of the protein; however, EAA digestibilities varied between the two feces collection systems.

Growth and Biochemical Analysis

Experiment 1

After 16 wk on the test diets in experiment 1, regression analysis indicated a significant linear regression ($r^2 = 0.98$) on final body weight of the CM content of the diet. The results suggest that for every level of CM inclusion in the diet there was a reduction in the final body weight of the fish, with each successive incremental level resulting in a greater depression. There were no significant differences in the feed to gain ratios, mortalities, and final carcass composition of the trout after 16 wk on the test diets (Table 3). Similarly, there was no significant difference in the hemoglobin, hematocrit, liver to body weight ratio (LBW), or carcass and liver zinc content of the trout after 16 wk on the test diets (Table 4). Serum T_3 and T_4 levels were not significantly different between the various groups of trout after 16 weeks on the test diets in experiment 1. However, while the results were extremely variable, there did appear to be a trend toward declining levels of serum T_3 and T_4 with increasing levels of dietary CM. Furthermore, there was no significant linear regression of dietary level of CM on T_3 and T_4 serum levels.

Experiment 2

After 16 wk on the test diets there was a significant reduction in the final body weight of trout reared on the CM-based diets in comparison with the trout fed the control diet (diet 1 vs. 2, 3, 4, Table 5). Supplementation with arginine, lysine and zinc (diet 3), or energy (diet 4) had no significant effect on cor-

TABLE 5. Final body weight, feed to gain ratios, mortalities, and final carcass composition of the trout after 16 wk on the test diets at 15°C in experiment 2 (canola meal replacement of fish meal) (results based on the mean of four tanks or samples per treatment ± SD).

	Diet number (% inclusion of canola meal)			
Parameter	1 (0)	2 (35)	3 (35)	4 (36)
Total body weight (g/fish)[a]	48.1±2.2 a	32.6±0.4 b	32.7±1.4 b	30.3±0.9 b
Feed:gain	1.1±0.1	1.2±0.1	1.2±0.1	1.1±0.0
Mortalities (%)	0	0.3±0.0	0.3±0.0	0.3±0.0
Carcass analysis[b]				
Protein	51.7	48.4	52.3	49.2
Lipid	41.4	44.6	41.3	43.0
Ash	5.9	5.3	5.7	5.5

[a]Initial weight 2.2 g/fish; results followed by the same letter are not significantly different.

[b]Results expressed on a dry matter basis.

TABLE 6. Pathological changes (1 = mild; 2 = moderate; 3 = severe; — = no abnormalities observed) observed in the thyroid glands of rainbow trout fed test dites 1–4 in experiment 1 and diets 2 and 4 in experiment 2 after 16 wk on the test diet.

Diet number (% CM)	Experiment	Microfollicles	Follicular hyperplasia	Pleomorphic follicles	Epithelial hyperplasia	Epithelial hypertrophy	Colloid vacuolated or depleted	Group total
1 (0)	1	—	—	—	—	—	—	0
2 (13.5)	1	—	1	1	1	2	1	6
3 (26.9)	1	2	2	1	1	1	1	8
4 (40.4)	1	3	2	1	2	1	3	12
2 (35)	2	1	1	—	1	1	1	5
4 (36)	2	2	1	2	1	2	1	9

recting the growth depression of the trout. Similarly, there was no significant difference in the final carcass analysis (Table 5), hemoglobin, hematocrit, LBW, or serum T_3 and T_4 levels (Table 4) of the trout reared on the different test diets. As in experiment 1, there was a decline in the serum T_3 and T_4 levels of the trout in the CM-based diets as compared with the trout reared on the control diet. However, the large variability in the results nullified any possible statistical significance.

Histopathology

External examination

All fish reared on the CM-supplemented diets had a very dark pigmentation in relation to the control groups in experiments 1 and 2. Four fish fed diet 4 in experiment 1 displayed a minor swelling and reddening of the tissues in the subbranchial region immediately adjacent to the ventral attachments of the gill arches. This affected area was confined to the zone between the gill arch bases and the scaled integument overlying the isthmus. All other groups were normal.

Trout reared on diet 1 in experiment 1 had histologically normal thyroid tissue. Low numbers of follicles were scattered diffusely throughout the loose aerolar connective tissue of the isthmus region. These follicles were circular in shape, with a single-cell-thick layer of squamous epithelium surrounding a lumena filled with homogeneous, lightly eosinophilic colloid material. However, a wide variety of histopathological changes were observed in trout reared on diets 2, 3, and 4 in experiment 1 and diets 2 and 4 in experiment 2. All of these groups exhibited varying degrees of six major types of changes directly involving the thyroid follicle. Abnormal thyroid tissue had increases in the amount of follicular epithelium (epithelial hyperplasia) or in the number of discrete follicles (follicular hyperplasia). In these same follicles, the epithelium was enlarged (epithelial hypertrophy) ranging from cuboidal to tall columnar with prominent, basally located nuclei. Follicle diameters tended to be smaller in abnormal thyroids (microfollicles) often displaying a wide range of sizes and noncircular shapes (pleomorphism), and many follicles were elongated or trabeculate in appearance. Hyperplastic thyroid tissue could be easily recognized by a dense aggregated mass of follicles and/or poorly organized epithelial cells occupying the aerolar, sub-branchial tissues. Colloid material in these abnormal glands was highly vacuolated or completely depleted within the follicles. When present, the colloid had a stippled, lightly eosinophilic to faintly basophilic appearance. The interstitial tissues were normally well-vascularized and showed no signs of inflammation.

In general, four major subdivisions of the six groups were evident (Table 6). Fish reared on diet 4 in experiment 1 had the most advanced pathological changes, displaying a diffuse, microfollicular hyperplasia with little or no colloidal reserves. Trout reared on diet 2 in experiment 1 and diet 4 in experiment 2 were moderately affected and not substantially different from one another. Trout reared on diet 3 in experiment 1 and diet 4 in experiment 2 were slightly more advanced, but again similar to each other, while trout reared on diet 1 in experiment 1 were normal.

Discussion

We conclude the CM should not, at this time, be included as a feed ingredient in commercial diets for young rainbow trout. Without further genetical improvement in either the specific cultivars of rapeseed or the processing of this vegetable protein meal, there would appear to be no economic advantage for its incorporation into trout diets. Furthermore, the inclusion of CM at this time may be detrimental to the growth and health of the fish.

The major limiting factor in the digestion of CM is the low dry matter digestibility of this feedstuff (Table 2). This is probably attributable largely to the relatively high crude fibre content (11.1%) of this product relative to soybean meal or fish meal; CM is also higher in other indigestible carbohydrates than soybean meal. It was a common observation that those fish feeding on the high CM-based diets in experiments 1 and 2 produced an excessive amount of feces. This could ultimately affect the water quality of the trout farm water supply by increasing the suspended solids and the biological oxygen demand. Obviously, this would reduce the carrying capacity of the aquatic system and be potentially hazardous to the health of the fish, since increased levels of suspended solids can inhibit respiration and encourage microbial growth on the gills of the fish, which can lead to bacterial gill disease (Wedemeyer et al. 1976). Although the protein digestibility of the CM was considerably lower than that of other protein meals analysed in our laboratories (Cho and Slinger 1979; Cho et al. 1982), the reduction in the availability of the EAA in the CM would probably not result in any overt EAA deficiencies in trout fed diets adequate in protein.

It may be noted (Table 2) that, in general, digestibility values were somewhat higher using the Guelph System than the rectal collection method. This is probably due mainly to nutrient losses related to water solubility and/or floatation of compounds with specific gravities lower than that of water, with the Guelph System. Because of this we consider the results based upon the rectal collection method to be more representative of actual digestibilities than those derived using the Guelph System. It seems unlikely that the difference in the size of the fish using the two methods would be responsible for the differences noted.

The results of experiment 1 indicate that CM cannot effectively replace soybean meal in commercial trout diets at the levels of 13.5% of the diet or greater. It is not immediately apparent why the results of this study are not in agreement with the studies of Yurkowski et al. (1978) and Hardy and Sullivan (1983). However, the fish used in the present study were much younger (and smaller) than fish used in the study of Hardy and Sullivan (1983). It is possible that younger fish are more sensitive to diets containing CM than are older fish. The CM contained 1.37 mg total glucosinolates/g and supplied from 158 to 509 μg total glucosinolates/g in experiment 1 and from 418 to 441 μg total glucosinolates/g to the CM-based diets in experiment 2 (Table 1). As in previous studies on CM utilization in salmonid diets (Yurkowski et al. 1978; Higgs et al. 1982), CM produced a diffuse, microfollicular hyperplasia in the thyroid tissues of the trout. The histopathological changes increased in relation to the level of CM incorporation, and the most advanced pathological changes occurred in trout reared on diet 4 in experiment 1 (Table 6), which had the highest CM supplementation level (Table 1). In addition, this group of fish was the only group displaying any overt or gross signs of goiter development. Despite the fact that there was no significant difference in the serum T_3 and T_4 levels in any of the groups of fish in this study (Table 4), it is apparent that the most adverse characteristic of CM is the level of glucosinolates that this product contains. Why there was no significant effect of the CM supplementation levels on the serum T_3 and T_4 levels is not readily apparent but may be due to the fact that the analysis was confined to a single sample which may not adequately reflect the dynamic thyroid hormone status (Hardy and Sullivan 1983). Although there was no significant effect of CM supplementation on serum T_3 and T_4 levels, the significant reduction in growth and the thyroid histological abnormalities of all the trout reared on the CM-based diets indicate that the glucosinolate levels present in the diets were toxic and exceeded tolerance limits. Therefore, we conclude that the tolerance level of dietary glucosinolates in young rainbow trout is less than 158 μg/g, the minimum level of glucosinolates supplied by the CM in this study. This is considerably less than the maximum 300 μg total glucosinolates/g diet suggested by Higgs et al. (1982) for chinook salmon and the 230–340 μg total glucosinolates/g diet used without effect in trout by Hardy and Sullivan (1983). It is possible that the young trout used in the present study are much more sensitive to dietary glucosinolates than either the salmon or the older trout used in the previous studies. This obviously warrants further study.

The present results indicate that CM cannot successfully replace even 10% of fish meal in practical diets for young rainbow trout (Table 5). Arginine and lysine are the most likely amino acids to be adversely affected by the various processing techniques applied to the CM and the fish diet (Linener 1980). In addition, Viola et al. (1982) indicated that there is a low availability of lysine in soybean meal to fish. However, the apparent digestibility of these two amino acids in the CM appeared to be essentially the same as that of the other EAA (Table 2). Furthermore, supplementation with arginine and lysine did not significantly increase the growth response of the trout. Therefore, the growth inhibition of the CM does not appear to be related to a reduction in the availability of arginine and lysine.

The supplementation of the CM-based diet with zinc (experiment 2, diet 3, Table 5) also did not significantly increase the growth response of the trout. Surprisingly, even though diet analysis indicated a higher zinc content of this diet (experiment 2, diet 3, Table 1), the liver and final carcass content of trout reared on the zinc-supplemented diet (diet 3) was not significantly different from the control groups (Table 4). This would indicate that zinc is not a factor in CM reducing growth. In addition, there were no overt signs of any cataract development or caudal fin erosion in the fish reared on the various test diets in this study. Previous studies have shown that these signs are characteristic of a zinc deficiency in fish (Ogino and Yang 1978; Ketola 1979).

Viola et al. (1982) indicated that the energy content of soybean meal was lower than that of fish meal in diets for fish. In their study, increasing the lipid supplementation of the diet increased the growth of the fish fed a diet containing soybean meal. In our study, the availability of energy from the CM was lower than that of soybean meal or fish meal as determined by Cho and Slinger (1979). However, the addition of extra energy to the CM-based diet (experiment 2, diet 4), in the form of herring oil, did not significantly improve the growth of the trout; in fact there was a slight, but not significant, reduction in the final body weight of these fish (Table 5). Therefore,

increasing the energy content of the CM-based diet with increased supplementation of lipid did not improve the utilization of CM as a protein source for rainbow trout.

The results in Tables 3 and 5 indicate clearly that growth was depressed when CM was used to replace either soybean meal or fish meal, while the feed to gain ratio was little affected. This suggests, and feed intake figures confirm, that one of the main reasons for the growth reduction with CM-supplemented diets is the fact that fish reduce their feed intake when offered such diets. Whether this is due to a lack of palatability or some other factor can only be determined by further work. However, it is well known that glucosinolates are bitter to the taste and result in reduced feed intake in several mammalian species.

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References

ATKINSON, J. L., J. W. HILTON, AND S. J. SLINGER. 1984. Evaluation of acid-insoluble ash as an indicator of feed digestibility in rainbow trout (*Salmo gairdneri*). Can. J. Fish. Aquat. Sci. 41: 1384–1386.

BLIGH, E. G., AND W. G. DYER. 1959. A rapid method of total lipid extraction and purification. Can. J. Biochem. Physiol. 37: 911–917.

CHO, C. Y., H. S. BAYLEY, AND S. J. SLINGER. 1974. Partial replacement of herring meal with soybean meal and other changes in the diet of rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 31: 1523–1528.

CHO, C. Y., AND S. J. SLINGER. 1979. Apparent digestibility measurement in feedstuffs for rainbow trout, p. 239–247. *In* J. E. Halver and K. Tiews [ed.] Finfish nutrition and fishfeed technology. Vol. II.

CHO, C. Y., S. J. SLINGER, AND H. S. BAYLEY. 1982. Bioenergetics of salmonid fishes: energy intake, expenditure and productivity. Comp. Biochem. Physiol. 73B: 25–41.

HARDY, R. W., AND C. V. SULLIVAN. 1983. Canola meal in rainbow trout (*Salmo gairdneri*) production diets. Can. J. Fish. Aquat. Sci. 40: 281–286.

HIGGS, D. A., J. R. MCBRIDE, J. R. MARKERT, B. S . DOSANJH, M. D. PLOTNIKOFF, AND W. C. CLARKE. 1982. Evaluation of tower and candle rapeseed (canola) meal and Bronowski rapeseed protein concentrate as protein supplements in practical diets for juvenile chinook salmon (*Oncorhynchus tshawytscha*). Aquaculture 29: 1–32.

HILTON, J. W., AND S. J. SLINGER. 1981. The nutrition and feeding of rainbow trout. Can. Spec. Publ. Fish. Aquat. Sci. 55: 15 p.

HILTON, J. W., J. L. ATKINSON, AND S. J. SLINGER. 1982. Maximum tolerable level, digestion, and metabolism of D-glucose (cerelose) in rainbow trout (*Salmo gairdneri*) reared on a practical trout diet. Can. J. Fish. Aquat. Sci. 39: 1229–1234.

1983. Effect of increased dietary fibre on the growth of rainbow trout (*Salmo gairdneri*). Can. J. Fish. Aquat. Sci. 40: 81–85.

HORWITZ, W. 1980. Official methods of analysis of the Association of Official Analytical Chemists. 13th ed. AOAC, Washington, DC. 1018 p.

KETOLA, H. G. 1979. Influence of dietary zinc on cataracts in rainbow trout (*Salmo gairdneri*). J. Nutr. 109: 965–969.

KOOPS, H., K. TIEWS, H. BECK, AND J. GROOP. 1976. Die Verwertung von Sojaperotein durch die Regenbogenforelle (*Salmo gairdneri*). Arch. Fischereiwiss 26: 181–191.

LANNO, R. P., S. J. SLINGER, AND J. W. HILTON. 1985. Maximum tolerable and toxicity levels of dietary copper in rainbow trout (*Salmo gairdneri*). Aquaculture 49: 257–268.

LEATHERLAND, J. F. 1983. Effect of ambient salinity, food deprivation and prolactin on the thyroidal response to TSH, and in vitro hepatic T_4 to T_3 conversion in yearly coho salmon, *Oncorhynchus kibutsch*. Acta Zool. Stockholm 63: 55–64.

LIENER, I. E. 1980. Toxic constituents of plant foodstuffs. Academic Press, New York and London. 502 p.

NOSE, T. 1971. Determination of the nutritive value of food protein in fish. III. Nutritive value of casein, white fishmeal and soybean meal in rainbow trout fingerlings. Bull. Freshwater Fish. Res. Lab. Tokyo Univ. 21: 85–98.

OBERLAS, D., AND B. F. HARLAND. 1977. Nutritional agents which affect metabolic zinc status, p. 11–24. *In* Zinc metabolism: current aspects in health and disease. Alan R. Liss Inc., New York, NY.

OGINO, C., AND G-Y. YANG. 1978. Requirement of rainbow trout for dietary zinc. Bull. Jpn. Soc. Sci. Fish. 44(9): 1015–1018.

REINHOLD, J. G., F. ISMAIL-BEIGI, AND B. FARADJI. 1975. Fiber vs. phytate as determinant of the availability of calcium, zinc and iron of breadstuffs. Nutr. Rep. Int. 12: 75–85.

STEEL, R. G. D., AND J. H. TORRIE. 1980. Principles and procedures of statistics: a biometrical approach. 2nd ed. McGraw-Hill Book Co., New York, NY. p. 172–288.

VIOLA, S., S. MOKADY, V. RAPPAPORT, AND Y. ARIELI. 1982. Partial and complete replacement of fishmeal by soybean meal in feeds for intensive culture of carp. Aquaculture 26: 223–236.

WEDEMEYER, G. A., F. P. MEYER, AND L. SMITH. 1976. Environmental stress and fish diseases (No. 5). *In* S. F. Snieszko and H. R. Axelrod [ed.] Diseases of fishes. T. F. H. Publ. Inc. Ltd., Toronto, Ont. 192 p.

YURKOWSKI, M., J. K. BAILEY, R. E. EVANS, J. L. TABACKEK, AND G. B. AYLES. 1978. Acceptability of rapeseed proteins in diets for rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 35: 951–962.

Current Velocity in Streams and the Composition of Benthic Algal Mats

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Reiter, M. A., and R. E. Carlson. 1986. Current velocity in streams and the composition of benthic algal mats. Can. J. Fish. Aquat. Sci. 43: 1156–1162.

Water velocity is commonly accepted as a factor in the development of benthic algal mats in streams. Within a stream, two different zones of velocity are observed: the free-water velocity of the open water and the local velocity near the stream substrate. A closed laboratory flume system was used to observe the taxonomic composition of benthic algal mats and corresponding changes in the local velocities under different free-water velocities. As the algal mat developed under each experimental velocity, local velocities diminished and eventually became equal in all sections, while free-water velocities remained different. After a period of maximum taxonomic diversity during the first 2 wk of mat development, taxonomic composition, relative abundance of the taxa, and dry weight biomass became increasingly similar in the three velocity regimes, although the mats appeared different upon casual observation. Differences in composition and morphology in natural algal mats may not result from differences in current velocity, and the idea of a "closed monolayer" algal mat may not be appropriate in all situations.

Il est généralement admis que, dans les cours d'eau, la vitesse de l'eau constitue un facteur dans la croissance des tapis d'algues benthiques. À l'intérieur d'un cours d'eau, on observe deux zones différentes de vélocité : la vitesse d'écoulement de la masse d'eau et la vitesse locale près du substrat du cours d'eau. On s'est servi d'un système clos de canaux en laboratoire pour observer la composition taxonomique des tapis d'algues benthiques et les changements correspondants dans les vitesses locales sous l'influence de diverses vitesses d'écoulement. À mesure que le tapis d'algues se développait sous l'influence de chaque vitesse expérimentale, les vitesses locales ont diminué et sont devenues éventuellement égales dans toutes les sections, alors que les vitesses d'écoulement restaient différentes. Après une période caractérisée par une diversité taxonomique maximale au cours des deux premières semaines de développement des tapis d'algues, la composition taxonomique, l'abondance relative des taxons et la biomasse en poids sec sont devenus de plus en plus semblables dans les trois régimes de vitesse, bien que les tapis d'algues aient semblé différents à première vue. Il se pourrait que les différences dans la composition et la morphologie des tapis d'algues naturelles ne résultent pas des différences observées dans la vitesse du courant et l'idée d'un tapis d'algues « fermé » en une seule couche pourrait ne pas d'appliquer à toutes les situations.

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Water velocity is commonly accepted as a factor affecting the growth of benthic algal mats in streams. Several investigators have documented differences in benthic algal species in areas of different water velocities (Butcher 1940; Whitford 1956; Blum 1956; Marker 1976; Horner and Welch 1981). McIntire (1968a) found, in a laboratory study, that an increase in current speed had a positive effect upon the growth of some species of algae, while other species were inhibited.

Patrick (1948) stated that fast water selected for diatoms having attachment mechanisms, while slower water allowed nonattached forms to grow. Whitford (1960) hypothesized that a velocity-related "diffusion shell" regulated the supply rate of nutrients to an algal cell. Some algae could utilize the low nutrient supply rates of slower water, while other algae required the greater supply rates found in faster water.

Whitford's hypothesis of the relationship between current velocity and nutrient availability has been studied in the laboratory (Whitford and Schumacher 1961, 1964; Schumacher and Whitford 1965), although studies have questioned the conditions over which it might apply (Lock and John 1979; Horner and Welch 1981; Antoine and Benson-Evans 1982). The studies suggest that different algae will grow in velocities which are most suitable to their nutrient supply requirements and growth forms (large or small; attached or unattached).

McIntire (1968b, 1973) made the transition from the single-species hypothesis of Whitford to the entire periphyton community by assuming a surface layer of living, active cells overlying a layer of dying or decomposing cells and detritus. The surface layer, the site of growth in this model, is subjected to velocities proportional to the velocity of the water layers above (free-water velocity). The growth of the community is dependent upon the supply of nutrients dictated by the free-water nutrient concentration and the free-water velocity. The community would be composed of species of similar nutrient uptake

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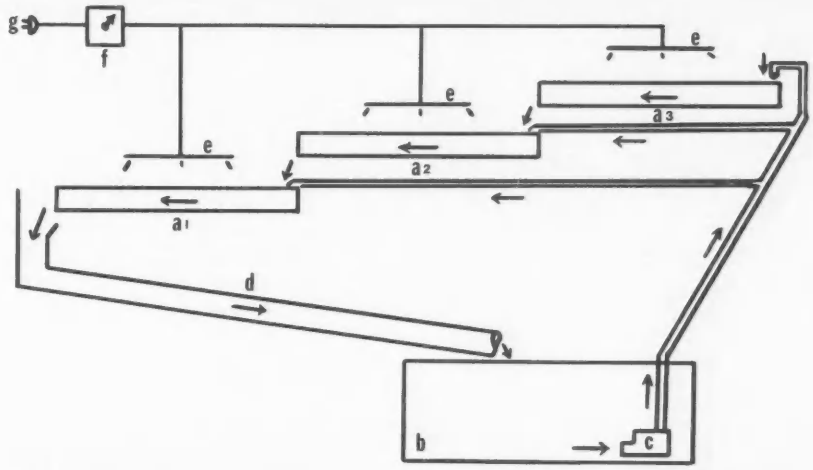

FIG. 1. Schematic drawing of the experimental apparatus: a, flume section and number; b, holding tank; c, water pump; d, return conduit; e, light source; f, timer; g, electric source; h, input conduit. Arrows represent the direction of flow.

kinetics. Within a stream section, where nutrient concentrations are similar, different flow regimes would result in distinct periphyton communities.

The present study concerns the actual relationships between the free-water velocities and the velocities in and near an algal mat (local water velocity) under similar nutrient concentrations. Preliminary experiments had suggested that similar algal communities develop regardless of the overlying free-water velocities. This led to the hypothesis that the algal mat itself modifies the water velocity, producing similar local water velocities, which leads to similar community composition.

Materials and Methods

A closed flume system was designed which permitted the control of water velocity and the observation of vertical microzones of velocity in and above the algal mat. The system consisted of a three-sectioned glass flume, each section being 1.2 m long, 12.7 cm high, and 3.76 cm wide (Fig. 1). Each section was attached to a wooden base, had the upper end closed, and had straight plastic strips placed vertically at the upper end to minimize nonlinear turbulent flow in the section. The substrate consisted of a 1.5-cm layer of hydrophyllic, waterproof epoxy (Cadco Ba-500), which gave a smooth, uniform surface. The final section emptied into a pipe which carried water to a covered 200-L fiberglass tank, which contained the water for the system. Water was recirculated to all three sections by means of a Little Giant submersible fountain pump through Tygon tubing. Water velocity in each section was a function of water input from the pump, water input from the previous section(s), and the slope of the section itself. Water from the holding tank entered all three sections directly, reducing the possibility of differential settling of certain algae in the upper sections.

For the experiment, the tank was filled with 200 L of water from Fish Creek (a third-order northern Ohio stream). Water lost by evaporation during the 7-wk experiment (approximately 25 $L \cdot wk^{-1}$) was replaced weekly with fresh stream water from Fish Creek. These additions of stream water, representing 12.5% of the total volume, were used instead of the addition of distilled water to ensure the introduction of potential colonizers into the experiment, and to maintain a semblance of natural nutrient levels.

Lighting was provided by one 15-W fluorescent lamp (G.E. Watt-Miser) suspended 25 cm over each section. The 24-h photoperiod was kept at that of the first day of the experiment (approximately 10 h of light). Some continuous light from the room entered through the glass walls of the flumes, but its effect was assumed to be small in comparison with the effect of the light source directly above the flume.

Nutrient concentrations were equal in all sections because water was pumped directly into all three sections, thus reducing the effects of depletion in upstream sections. The soluble reactive phosphorus concentration, measured 3 d after the weekly additions of water, was 47–57 $\mu g\ P\text{-}PO_4 \cdot L^{-1}$, except for the first 2 d of the experiment, when concentrations were almost twice as high. The concentrations did not vary in any systematic manner throughout the experiment. The pH of the water remained at 6.1 throughout the experiment. Macrograzers, such as chironomids, snails, and other invertebrates, were removed when seen. Water was at room temperature (approximately 22°C) during the experiments.

Uniform circular (0.2 cm^2) samples of the algal mats were taken weekly from the sections using a sharp-edged glass tube attached to a suction device (Glasfirn pi pump Gr10). The opening of the tube was placed on the mat, rotated, and moved along the substrate to loosen the mat sample, which was then sucked into the tube. The algae from equal numbers of transect fields from each sample were counted microscopically by focusing through the mat and counting each plane of cells. At least 200 individual cells of subdominant genera were counted, often requiring the counting of over 1000 total cells. Individual cells of filamentous species were counted. Total cell volume was calculated by multiplying the number of cells of each species by a coefficient determined by the geometric approximation of the cell volume. The dry weight biomass was measured as the weight of a sample dried at 100°C for 24 h. The in situ height of the algal mat was determined by measuring

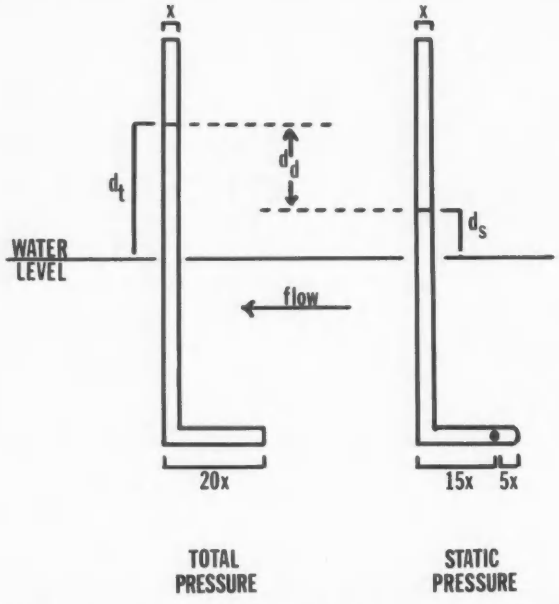

FIG. 2. Schematic drawing of total and static pressure tubes (modified from Benedict 1977): x, external diameter; d_t, displacement due to total pressure; d_s, displacement due to static pressure; d_d, displacement due to dynamic (motion) pressure.

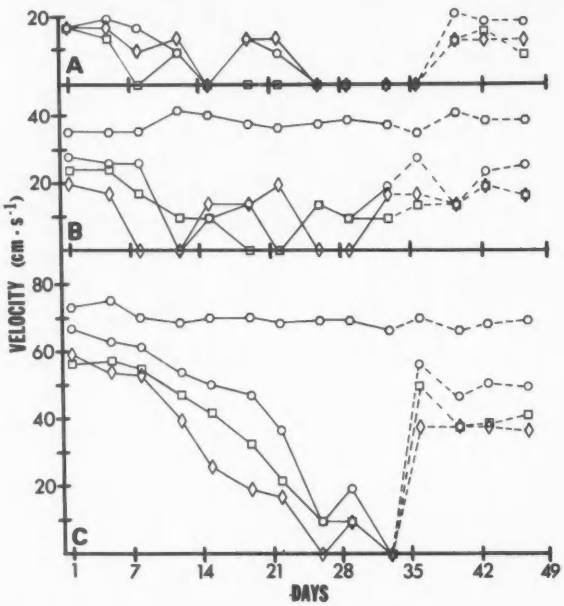

FIG. 3. Values of velocity at measurement site 2 (midflume) for (A) section 3, (B) section 2, and (C) section 1. ◇, 0.7 mm above the substrate; □, 2.2 mm above the substrate; ○, 3.7 mm above the substrate; ⬭, free-water velocity. Solid lines indicate a site with an unsloughed mat; broken lines indicate a site with a sloughed mat.

several locations in each section with a ruler and recording the average.

Design and Use of Pitot Tubes

Pitot tubes are a simple but useful means of measuring velocities in very small areas. Crude forms of these tubes have been used in the past when dealing with the layers of velocity affecting benthic invertebrates (e.g. Grenier 1949). As Hynes (1970) and Benedict (1977) pointed out, this method has some difficulties, can be imprecise, and is most accurate in a linear flow of a known direction. In our experiment, these problems were minimized by using a smooth substrate, flow regulators, and correction factors for the Pitot tubes.

One set of total pressure tubes and one set of static pressure tubes were made of square-ended glass capillary tubing (diameter 1.5 mm) according to the specifications of Benedict (1977) (Fig. 2). These tubes were calibrated against constant velocities, providing a correction factor that was used to correct measurements taken with the individual tubes.

The tubes were placed at the point to be measured and the capillary distance (the distance the water in the tube exceeded the surface of the water in the section) measured to the nearest 0.5 mm using a ruler attached to the outside of the glass wall. The difference between the height of the total pressure tube column (caused by water movement and static pressure) and the static pressure tube column (caused by static pressure and other extraneous factors) after correction gave the pressure change caused by the movement of the water. This height was converted to a point water velocity using the equations of Benedict (1977). Water temperature values necessary to calculate water density (Weast and Astle 1982) and specific weight (Benedict 1977) were taken with a mercury thermometer.

The theoretical velocity curve for Pitot tube measurements based on the Benedict equations indicates that this technique is more sensitive to velocity changes at higher velocities than at lower velocities. Changes in capillary height of 0.5 mm at low velocities means in some cases a change in velocity value of up to 9 $cm \cdot s^{-1}$. Although this insensitivity at low velocities could be a major problem if extreme accuracy were necessary or if actual velocity values were important, only a relative measurement was needed in this study. The technique gives a reasonably accurate measurement of a point velocity in a very small area with relative ease.

Velocity measurements were taken at three locations within each section twice each week. At each location, "local" (near or within the algal mat) water velocity was measured at three heights (0.7, 2.2, and 3.7 mm above the substrate). An additional measurement was taken 0.5 cm from the water surface for "free-water" (open water) values. This value was not necessarily the maximum velocity of the section, but a standard value to be compared with the local velocity values. No free-water values were measured in section 3, as the point 0.5 cm from the surface was too close to the mat to be unaffected by local velocity alteration. Each velocity value obtained was the result of repeated readings at the level until three identical values were obtained (in all cases, no more than five attempts were necessary). The algal mats eventually sloughed at all velocity measurement points, but enough of the original mat remained in other parts of the sections to allow sampling of both the new and older growths.

Results

The initial free-water velocities of the three sections were as

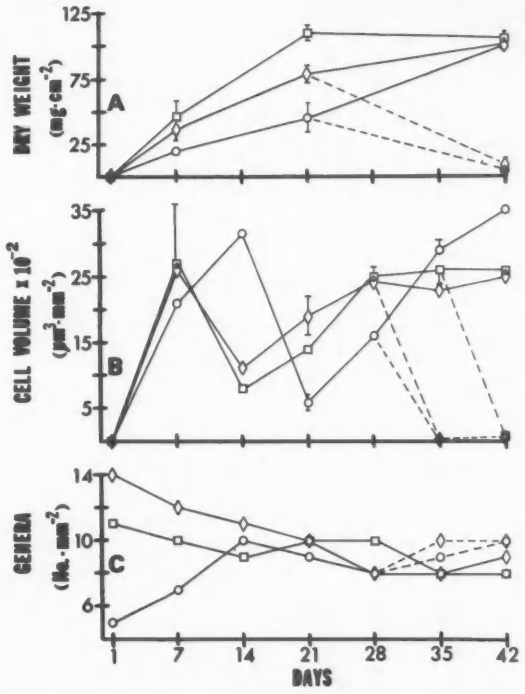

FIG. 4. Changes in (A) dry weight biomass, (B) total cell volume, and (C) number of genera for section 1 (○), section 2 (□), and section 3 (◇). Solid and broken lines as in Fig. 3. Values given are mean ± 1 SE.

follows: section 1, 71 cm·s^{-1}; section 2, 42 cm·s^{-1}; section 3, 20 cm·s^{-1}. The free-water velocities remained different and relatively constant throughout the experiment, except for those values measured in section 3, which were too close to the mat to be unaltered by local velocity (Fig. 3). Local water velocities slowed with time until similar local velocities were reached in all three sections. The sloughing of the algal mat later resulted in a reversion to higher local water velocities.

Casual observation of the algal mats in the three sections at the end of the experiment suggested that there were differences in the amount and kind of algae present. The slowest section, section 3, had a final average mat height of 1.5 cm and was composed of coiled filaments loosely attached to the substrate. Section 2 had a final average mat height of 1.0 cm, and the coiled filaments appeared to be shorter and more closely attached to the substrate. In both sections 2 and 3, the algae appeared to be somewhat patchy in distribution, and the entire mat had a light brown color. In contrast, section 1, the section having the fastest water velocities, had a final average mat height of 0.6 cm and had short, straight, firmly attached filaments, evenly distributed over the substrate. In this section, the mat had a blue–green color.

In contrast with the above observations, the values of dry weight biomass, total cell volume, and the total number of genera present in the three sections became increasingly similar with time (Fig. 4A–4C). Initially the taxonomic composition of the algal mats in all sections was quite dissimilar. More genera were found in the slower sections (Table 1), but many of these genera did not persist throughout the experiment.

TABLE 1. Genera found in the experiment by section number (P = present at some time during the experiment; D = present and dominant at the end of experiment).

Genus	Section 1 (fast)	Section 2 (intermediate)	Section 3 (slow)
Achnanthes		P	P
Ankistrodesmus		P	P
Asterionella		P	P
Cocconeis	P		P
Closterium			P
Cymatopleura	P	P	P
Euglena		P	P
Fragilaria		P	P
Melosira	D	D	D
Navicula	P	P	P
Nitzschia	P	P	P
Oscillatoria	P	P	P
Pinnularia	P	P	P
Rhoicosphaenia			P
Surirella		P	P
Synedra	P	P	P
Tabellaria	P	P	P
Ulothrix		P	P

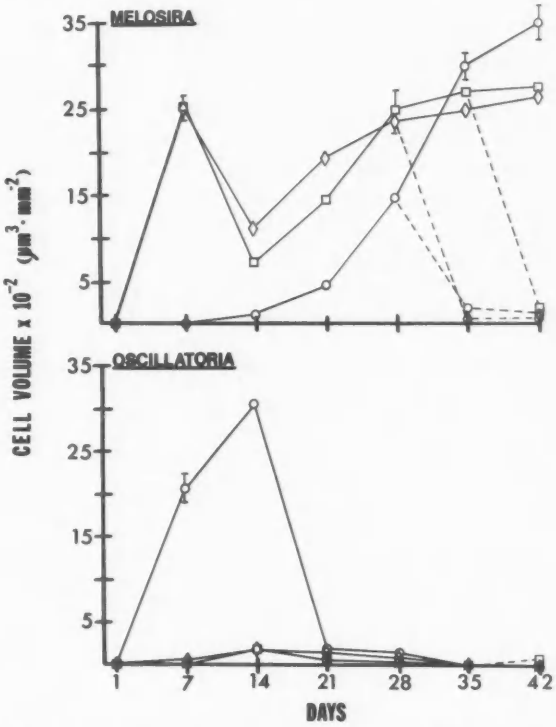

FIG. 5. Mean total cell volume (± 1 SE) of *Melosira* and *Oscillatoria*. Symbols and lines as in Fig. 4.

In sections 2 and 3, with local velocities below 45 cm·s^{-1}, *Melosira* dominated from the beginning. *Oscillatoria* initially dominated in section 1, but was replaced by *Melosira* (Fig. 5). *Melosira* did not dominate in this faster section until the local velocities approached 45 cm·s^{-1}. The increase in volume per

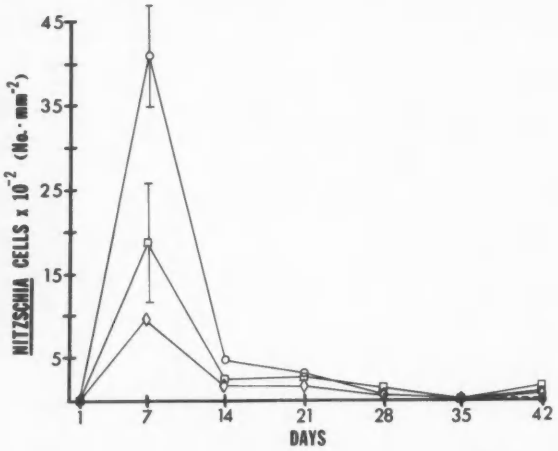

FIG. 6. Total numbers of cells (± 1 SE) for a representative subdominant genus (*Nitzschia*). Symbols and lines as in Fig. 4.

cell from a mat of *Oscillatoria* to one of *Melosira* may explain why the total cell volumes in section 1 seemed to be "out of phase" with respect to the other sections (Fig. 4B).

The balance of the mats' species composition was primarily diatoms of four genera: *Nitzschia*, *Navicula*, *Tabellaria*, and *Synedra*. The maximum numbers of each of these genera were reached by the second week of the experiment, after which their numbers declined (Fig. 6). The subdominant genera showed no consistent pattern in dominance in any of the sections.

The similarity of the algal mats is substantiated by the use of the "community overlap" index of Horn (1966). This index, which compares two communities in terms of both the number of taxa common to both communities and the relative abundance of these taxa, indicates a trend toward similarity in community composition (Table 2). Table 2 also indicates a period of minimum similarity prior to 14 d of growth. Taxonomic similarity between sections was greatest in the older, unsloughed mat areas where local velocities were similar for longer periods of time.

A similar experiment was conducted on water from Allerton Creek, a first-order stream on the campus of Kent State University. The experiment was conducted in a manner similar to that described above, using the same apparatus and environmental conditions. The initial parameters for this experiment are given in Table 3. The results of this experiment are similar to those described for waters from Fish Creek (Reiter 1983). The local water velocities decreased to similar levels by the end of 5 wk, and as was seen in the other experiment, the relative composition and abundance of algae, the total number of cells, and the number of genera became similar. The final algal composition in the mats was markedly different from that seen in the Fish Creek experiment, suggesting that these experiments are demonstrating a universal phenomenon rather than the effect of a specific algal community.

Discussion

Past research has given us a reasonable hypothesis of how current velocity causes variation in algal community structure in streams. Our results suggest that these ideas may not apply to all types of attached algal communities or situations.

TABLE 2. Horn (1966) "community overlap" index values for unsloughed mat samples (0 = least; 1 = most).

Days	Sections compared: Fast−int. (1 vs. 2)	Int.−slow (2 vs. 3)	Fast−slow (1 vs. 3)
1	0.55	0.80	0.65
7	0.85	0.94	0.69
14	0.78	0.98	0.73
21	0.64	0.98	0.67
28	0.74	0.99	0.70
35	0.92	0.99	0.95
42	0.99	0.99	0.99

According to the hypotheses of Whitford (1960) and McIntire (1968b, 1973), different free-water velocities have proportionally different local velocities at the mat surface. Thus, when different species of algae are seen growing in slower pools or faster riffles, present ideas suggest that the algae themselves are experiencing differences in velocity. Whitford's (1960) diffusion shell hypothesis suggests that the algae growing in a given area should be those species best suited to the velocity-controlled nutrient supply of that area.

In contrast, this study presents a situation in which differences in free-water velocity do not translate directly into proportional differences in local velocity. Algal growth seemed to increase physically the frictional surface of the substrate, creating an increase in the thickness of the laminar sublayer. Over time, all but the very surface of the mat was within relatively slow local velocities. Only the mat surface experienced anything proportional to the free-water velocity of the current, and even there the velocity was reduced. Where the present concept predicted different local velocities and different dominant algal species, we observed increasingly similar local velocities and similar dominant algal species. Casual observation of the algal mats gave no hint of this similarity. It seems possible that the gross appearance of an algal mat could be determined more by environmental factors related to free-water velocity than by the genera which compose the mat. These results suggest that caution should be used when assuming that two algal communities which appear different in the field are actually composed of different species.

It seems possible to present a modified hypothesis concerning the effects of velocity upon benthic mat growth. In this hypothesis, algal mat growth eventually creates a situation where the velocities near and within the algal mat (local velocities) become similar independent of their free-water velocity counterparts. These local velocities, in tending toward zero, create a similarity in current effects and diffusion shell effects, producing over time similar mats (similar species, similar morphological forms, similar biomass, etc.). If applied to field situations, this would suggest that attached algal communities in a given stretch of stream, if undisturbed, should be converging in terms of numbers, biomass, and species composition.

This hypothesis is not necessarily a contradiction of the observations of species distributions in streams, as factors other than local water velocity could affect the algal community composition. In this experiment, little of the turbulence that would be expected in a natural stream was present. The changes in direction of flow, shear force, and pressure caused

TABLE 3. Comparison of key conditions and results between the Allerton Stream and Fish Creek experiments. Values represent all unsloughed sites.

Condition or result	Allerton Creek			Fish Creek		
Replacement of evaporated water	Weekly, distilled			Weekly, stream		
Maximum flow depth (cm)	6			5		
Free-water velocity ($cm \cdot s^{-1}$)	83	53	42	73	36	18
Local water velocity						
Initial values, level 1 ($cm \cdot s^{-1}$)	68	51	42	57	21	16
Final values, level 1 ($cm \cdot s^{-1}$)	24	20	14	0	9	0
Number of genera						
Largest range	5	11	17	5	11	14
	(day 5)			(day 1)		
Final values	5	6	9	8	8	9
Percent (by numbers) of dominants in mat						
Largest range	66	72	24	0	72	45
	(day 5)			(day 1)		
Final values	99	91	93	96	96	93
Dominant genera	*Tolypothrix* *Oscillatoria*			*Melosira* *Oscillatoria*		

by turbulent flow could alter the pattern of development seen in our study. Although turbulence could alter our results, the effect may be minor, as mat growth may eventually eliminate turbulence and small variations in flow near the mat. It should also be pointed out that turbulence very close to the substrate may often be a laminar flow. The effects of turbulent flow on the growth of attached algal mats should be a topic for future study.

Perhaps a greater difference between our results and existing hypotheses is that, in our experiment, the algal mats were dominated by filamentous algae. As both McIntire (1973) and Lock and John (1979) suggested, filamentous forms may present special cases. Filamentous mats may be different from the "outer monolayer" mat, as they allow for the expansion of the boundary layer by their growth while at the same time presenting an "open weave" mat which allows for colonization within the mat as well as on the surface. If most of the colonization in our experiment took place within the mat where velocities were similar, the diffusion shell hypothesis of Whitford (1960) would predict that similar mats should result, as the nutrient kinetics in these areas would be similar.

In our experiment, local velocities were proportional to free-water velocities during the first 2 wk of mat development. In this period, the species composition could have been affected by the free-water velocity. If, in field situations, the mat were continually disturbed before this early period passed, Whitford's hypothesis could be a valid explanation of species distribution. Disturbance of the algal mat in a stream could also result in the formation of patches of various ages. The actual control for creating this spatial variation could come from spate events, differential grazing, or seasonal changes in the algal species available to colonize new patches. It is worth noting that some of these factors may themselves be correlated with water velocity.

The role of water velocity on the growth of benthic algae may be limited by local velocity conditions, in the modification of which the algae themselves play a major role. If this is correct, much of the past literature was both correct and yet misleading. In our experiment, benthic algae did appear to be sensitive to water velocity, but the inevitable alteration of the algae's surroundings (including the immediate current velocity) by their growth made this sensitivity meaningless when invoking current velocity as the reason for the variety of algae found in different parts of a stream. The algae in our experiment did grow in mats, but not in a closed, dead layer with some live cells on top. These results suggest that there may be a strong need to define, if not reexamine, our present concept of benthic algal growth in streams. If this is done wth the realization that a dense mat as we see it is not necessarily a dense mat to an alga, and that a fast current velocity as we perceive it is not necessarily a fast current velocity in relation to a microorganism, then perhaps more relationships such as those presented here will become apparent.

Acknowledgments

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References

ANTOINE, S. E., AND K. BENSON-EVANS. 1982. The effect of current velocity on the rate of growth of benthic algal communities. Int. Rev. Gesamten Hydrobiol. 67: 575–583.

BENEDICT, R. P. 1977. Fundamentals of temperature, pressure, and flow measurement. 2nd ed. John Wiley & Sons, New York, NY.

BLUM, J. L. 1956. The ecology of the river algae. Bot. Rev. 22: 291–341.

BUTCHER, R. W. 1940. Studies in the ecology of rivers IV: Observations on the growth and distribution of the sessile algae in the river Hull, Yorkshire. J. Ecol. 28: 210–223.

GRENIER, P. 1949. Contribution à l'étude biologique des simuliides de France. Physiol. Comp. Oecol. 1: 165–330.

HORN, H. S. 1966. Measurement of "overlap" in comparative ecological studies. Am. Nat. 100: 419–424.

HORNER, R. R., AND E. B. WELCH. 1981. Stream periphyton development in relation to current velocity and nutrients. Can. J. Fish. Aquat. Sci. 38: 449–457.

HYNES, H. B. 1970. The ecology of running waters. University of Toronto Press, Downsview, Ont.

LOCK, M., AND P. JOHN. 1979. The effect of flow patterns on uptake of phosphorus by river periphyton. Limnol. Oceanogr. 24: 376–383.

MARKER, A. F. H. 1976. The benthic algae of some streams in southern England I: Biomass of the epilithion in some small streams. J. Ecol. 64: 343–358.

MCINTIRE, C. D. 1968a. Structural characteristics of benthic algal communities in laboratory streams. Ecology 49: 520–537.

1968b. Physiological–ecological studies on bethic algae in laboratory streams. J. Water Pollut. Control Fed. 40: 1940–1952.

1973. Periphyton dynamics in laboratory streams: a simulation

model and its implications. Ecol. Monogr. 43: 399–420.

PATRICK, R. 1948. Factors affecting the distribution of diatoms. Bot. Rev. 14: 473–524.

REITER, M. A. 1983. Interactions between local current velocity and benthic algal mat growth. M.S. thesis, Kent State University, Kent, OH. 101 p.

SCHUMACHER, G. J., AND L. A. WHITFORD. 1965. Respiration and P^{32} uptake in various species of freshwater algae as affected by a current. J. Phycol. 1: 78–80.

WEAST, R. C., AND G. A. ASTLE. 1982. Handbook of chemistry and physics. 62nd ed. CRC Press, Cleveland, OH.

WHITFORD, L. A. 1956. The communities of algae in the springs and spring streams of Florida. Ecology 37: 433–442.

1960. Current effect and the growth of fresh-water algae. Trans. Am. Microsc. Soc. 79: 302–309.

WHITFORD, L. A., AND G. J. SCHUMACHER. 1961. Effect of current on mineral uptake and respiration by a freshwater alga. Limnol. Oceanogr. 6: 423–425.

1964. Effect of a current on respiration and mineral uptake in *Spirogyra* and *Oedogonium*. Ecology 45: 168–170.

Effects of Environmental Variables on Growth Rates and Physiological Characteristics of Lake Superior Phytoplankton

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Nalewajko, C., and D. Voltolina. 1986. Effects of environmental variables on growth rates and physiological characteristics of Lake Superior phytoplankton. Can. J. Fish. Aquat. Sci. 43: 1163–1170.

Phytoplankton taxonomic composition and biovolume, assimilation numbers (P_m^B), phosphorus kinetics, as well as some physical and chemical variables were measured on 37 occasions during six cruises on Lake Superior during May 1980 – October 1981. A larger number of significant differences were detected between thermally stratified and isothermal stations than between inshore and offshore, or among seasons. Phytoplankton from isothermal waters was characterized by lower assimilation numbers and biovolume, showed symptoms of adaptation to a lower light regime, and was less phosphorus deficient than populations from thermally stratified waters. The lower growth rates and the outcome of stepwise multiple regression analyses suggest that phytoplankton growth during isothermal mixing is limited primarily by light.

On a évalué la composition taxonomique du phytoplancton et mesuré le biovolume, les taux d'assimilation (P_m^B), la cinétique du phosphore de même que certaines variables chimiques et physiques à 37 occasions lors de 6 expéditions faites sur le lac Supérieur de mai 1980 à octobre 1981. On a décelé un plus grand nombre de différences importantes entre les stations isothermiques et stratifiées thermiquement qu'entre les stations côtières et hauturières ou entre les saisons. Le phytoplancton des eaux isothermiques était caractérisé par des taux d'assimilation et un biovolume plus faibles, montrait des signes d'adaptation à un régime d'éclairage plus faible et était moins pauvre en phosphore que les populations des eaux stratifiées thermiquement. Les taux de croissance plus faibles et le résultat d'analyses de régressions multiples par étapes donnent à penser que la croissance du phytoplancton au cours du mélange isothermique est limitée surtout par la lumière.

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The premise that phosphorus is the primary factor controlling the trophic status of oligotrophic lakes has been unequivocally demonstrated (e.g. Schindler 1974), but our understanding of how physical factors such as light and temperature can modulate this productivity–phosphorus relationship is far from perfect. In Lake Superior, concentrations of total and soluble reactive phosphorus are very low, and the oligotrophic nature of the lake is without question (Schelske and Callender 1970; Schelske et al. 1972; Munawar et al. 1978; Nalewajko et al. 1981); however, a thermal regime characterized by maximal temperatures <16°C, and long periods of isothermal mixing (Bennett 1978), and the incidence of photosynthetic characteristics symptomatic of light limitation (Nalewajko et al. 1981), prompted us to examine the role of temperature and light history in controlling phytoplankton abundance and physiological characteristics. The importance of thermal stratification to Lake Superior phytoplankton was noted by Munawar and Munawar (1978) who found that spatial differences in phytoplankton species and biomass were not as large as differences between stratified and unstratified stations. Although inshore and offshore areas of Lake Superior do not differ as much as in the Lower Great Lakes (Munawar and Munawar 1978) where the thermal bar phenomenon is very pronounced, we chose to examine inshore areas, defined as 5 km from shore, separately from offshore because of differences in water depth, mean and maximum annual temperature, and the duration of thermal stratification between these areas. Also, phosphate turnover time is shorter inshore than offshore (Shear et al. 1981), which suggests a difference in the phosphorus status of the microbial populations. Our inshore areas correspond to zone 3 of the IJC Upper Lakes Reference Group (1977) and regions I, II, and IV of Munawar and Munawar (1978), while offshore corresponds to zone 13 and region V.

Our objective was to test the hypothesis that the different physical regimes during isothermal and stratified periods (as well as inshore compared to offshore) lead to differences in phytoplankton population density, species composition, physiological characteristics, and growth rates.

Methods

The data reported here were collected at 37 stations (Fig. 1) during six cruises during May 1980 – October 1981. The samples used for experiments were either taken with a 0–10 m vertical sample integrator or consisted of equal parts of discrete samples taken at 1-m intervals from 0 to 10 m with standard Van Dorn bottles. After sampling, aliquots were drawn for

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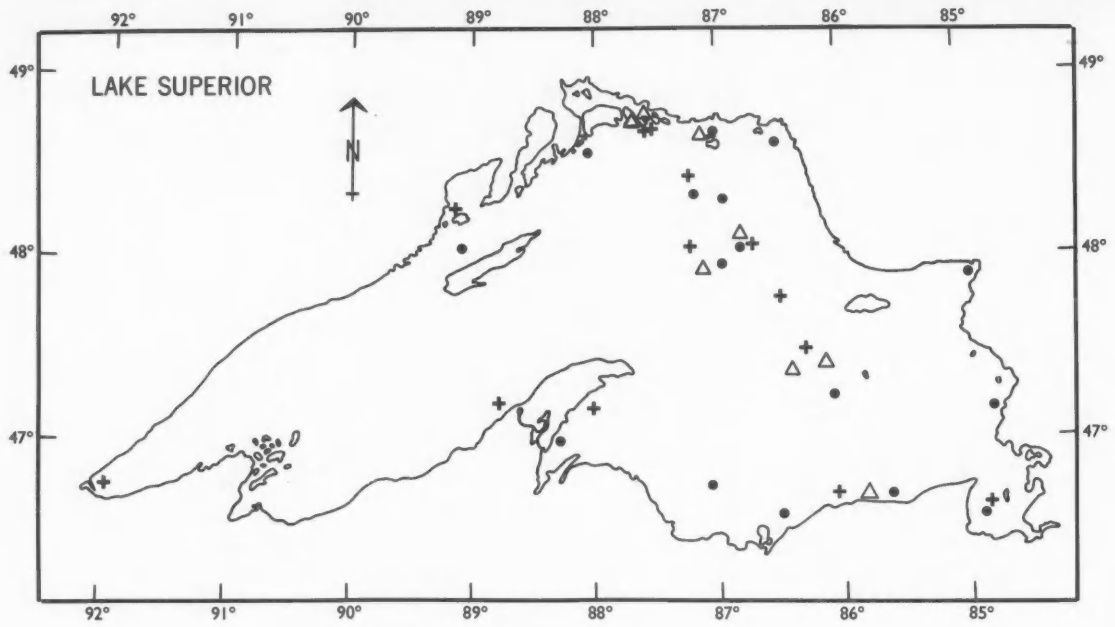

FIG. 1. Station location: ●, May–June; +, July; △, October.

experiments and for total phosphorus, alkalinity, and chlorophyll *a* analyses. The chemical analyses were carried out at the Water Quality Branch Laboratory, Canada Centre for Inland Waters, using standard procedures (Environment Canada 1979). Subsamples were also preserved with acidified Lugol's solution for phytoplankton enumeration according to the Utermohl method. Biovolumes were calculated from measurements of at least 20 cells for each species by approximation to geometrical figures.

All glassware was acid washed in dilute H_2SO_4 (about 20 mmol·L^{-1}), rinsed well with double-distilled water, sterilized by heating at 105°C, and stored dry.

To measure photosynthesis, 0.925 MBq of ^{14}C-$NaHCO_3$ was added to 400-mL subsamples of lake water in 500-mL Pyrex bottles. These were placed in an incubator at ambient lake water temperature. In 1980 we used an incubator fitted with high-output fluorescent lights (Canadian General Electric F48PG17/CW); the bottles were located above the lights. In 1981 we used an incubator in which bottles are illuminated from the side by quartz–halogen lamps (Philips 12013R). Neutral density screens were used to attenuate light reaching the bottles. Photosynthetically available radiation (400–700 nm) was measured with a Li-Cor quantum meter at the bottom of the bottle in 1980, and side in 1981. Every hour, for 4 h, 50-mL aliquots were drawn from each bottle, filtered on 47-mm, 0.45-μm pore size cellulose acetate filters, and rinsed twice with filtered lake water. The wet filters were placed in scintillation vials, and after addition of 15 mL of PCS liquid scintillation cocktail, their radioactivity was measured in a Beckman model 230 scintillation counter. The photosynthetic characteristics of the samples were then obtained by standard transformations. Assimilation numbers (P_m^B) were calculated as the ratio of P_{max} (micrograms C per litre per hour) to chlorophyll *a* (micrograms Chl *a* per litre). Growth rates, as doublings per day, were calculated as in Côté and Platt (1983).

To estimate the proportion of carbon uptake by organisms <1 μm, ^{14}C uptake of the phytoplankton fraction retained by 1-μm pore size Nuclepore filters was compared with total population uptake as measured by filtration on 0.2-μm polycarbonate or 0.45-μm cellulose acetate filters.

Rate constants of phosphate uptake were measured by following the uptake of carrier-free ^{32}P-PO_4 over 0.5–2 h (Lean and Nalewajko 1979) in the dark, at ambient lake water temperature. Other details are given in Nalewajko et al. (1986). The Michaelis–Menten parameter V_{max} was estimated from phosphate enrichment experiments, 0.1–2 μg P-PO_4·L^{-1} as in Nalewajko and Lean (1978).

Results

On a seasonal basis (Table 1) the biological variables we measured in Lake Superior are remarkably constant. P_m^B was significantly higher in October than in May–June, while chlorophyll *a* showed the opposite result. Growth rates, calculated from values of P_m^B, chlorophyll concentration, and hours of daylight (Côté and Platt 1983), were significantly higher in October than in May–June. When the data were grouped into inshore and offshore sets, only phosphate turnover time emerged as significantly different, much shorter values (3.9 h) occurring inshore than offshore (12.0 h). Since we hypothesized that vertical temperature stratification would have important implications for the phytoplankton, we sorted the results into stratified or isothermal groups (Table 1, C). P_m^B, P_{max}, and phytoplankton biovolume were significantly higher and phosphate turnover time significantly shorter in stratified than in isothermal water. Growth rates in stratified water were more than double the values in isothermal water.

There were no significant differences in the mean annual contribution of different algal groups to phytoplankton biovolume (Table 2) between inshore and offshore stations. Strati-

TABLE 1. Lake Superior May 1980 – October 1981. Data arranged by (A) inshore (<5 km from shore) and offshore stations, (B) season, and (C) thermally stratified and isothermal. Values shown are means. Within each of the three groups (A, B, C), Duncan's multiple range tests were used to identify means different at $P < 0.05$: these are indicated by — or ---.

	A		B			C	
	Inshore	Offshore	May–June	July	October	Stratified	Isothermal
Assimilation number (P^B_m)	2.19	1.63	0.39	2.02	2.88	2.52	1.23
P_{max} ($\mu g\ C \cdot L^{-1} \cdot h^{-1}$)	1.65	0.95	0.91	1.89	1.41	1.98	0.91
α ($\mu g\ C \cdot L^{-1} \cdot h^{-1}$) ($100\ \mu E \cdot m^{-2} \cdot s^{-1}$)$^{-1}$	0.57	0.47	0.54	0.40	0.77	0.53	0.50
Chl *a* ($\mu g \cdot L^{-1}$)	0.95	0.74	1.20	0.88	0.56	0.79	0.99
Phytoplankton ($10^6\ \mu m^3 \cdot L^{-1}$)	217.0	174.2	177.2	221.4	223.4	243.3	164.6
Total phosphorus ($\mu g \cdot L^{-1}$)	4.6	3.6	4.0	4.2	4.4	4.6	3.8
Phosphate turnover time, dark (h)	3.9	12.0	9.3	2.9	8.8	1.6	11.3
Temperature (°C)	7.6	5.0	3.0	10.9	6.6	10.7	3.6
Sunshine (h in previous 3 d)	19.6	20.3	21.2	27.6	7.4	21.6	18.6
Time of day	12:24	11:42	11:25	9:10	13:10	12:12	12:06
Depth (m)	89.3	206.2	152.0	126.9	133.7	98	168.4
Sample size	22	15	16	13	8	22	15
Onset of light-inhibited photosynthesis, 1981 data only ($\mu E \cdot m^{-2} \cdot s^{-1}$)	315–790	100–320	100–315	580–790	220–320	220–790	100–315
Growth rate μ (doublings $\cdot d^{-1}$)	0.39	0.23	0.15	0.44	0.65	0.51	0.22

TABLE 2. Mean annual contribution (%) of various algal groups to total phytoplankton biovolume (A) inshore and offshore; (B) by season, and (C) in thermally stratified and isothermal waters of Lake Superior, May 1980 – October 1981. Duncan's multiple range tests were used to identify means different at $P < 0.05$ within each group. These are indicated by — or ---.

	A		B			C	
	Inshore	Offshore	May–June	July	October	Stratified	Isotherma
Microalgae[a]	13.9	14.6	16.6	10.5	7.9	7.0	17.5
Bacillariophyta	35.4	28.7	40.8	28.0	17.4	29.0	35.2
Chlorophyta	31.4	28.3	24.8	38.5	16.1	34.8	26.4
Chrysophyta	5.6	6.9	2.3	5.7	23.7	9.8	3.7
Cryptophyta	4.5	8.5	3.5	7.0	15.2	7.9	4.7
Cyanophyta	6.8	7.8	7.3	7.6	10.7	6.9	7.4
Pyrrophyta	4.2	8.0	4.0	7.2	9.1	7.5	4.3

[a]Mainly flagellates <5 μm in size.

fied areas differed from isothermal only in the lower proportions of microalgae. Largest differences in species composition were apparent among the three seasonal groups: the proportion of diatoms was highest in May–June, green algae in July, and chrysophytes and cryptophytes in October.

In four of nine size-fractionation experiments, a significant difference (*t*-test, $P < 0.05$) was detected in phytosynthesis rates measured on 1- and 0.2-μm pore size filters. The greater radioactivity retained on 0.2-μm than on 1-μm pore size filters is an indication that autotrophic, picoplankton-size algae are present; however, only a fraction of picoplankton, generally defined as organisms <2 μm in size, passes the 1-μm pore size filter, so their contribution cannot be estimated accurately.

In May (Fig. 2A and 2B), the shape of the photosynthesis – light intensity curves of the >1 and <1 μm size fractions was similar, but in July (Fig. 2C and 2D) the <1 μm or picoplankton fraction exhibited light-inhibited photosynthesis at lower light intensities than the >1 μm fraction. Phytoplankton at the two stations sampled in May shows symptoms of low light adaptation. P_{max} was reached at about 35 $\mu E \cdot m^{-2} \cdot s^{-1}$, and light inhibition was apparent at intensities exceeding about 200 $\mu E \cdot m^{-2} \cdot s^{-1}$. On these four occasions picoplankton, at its P_{max}, accounted for about 20–50% of total phytoplankton photosynthesis, but this contribution decreased at higher light intensities. In five other size fractionation experiments, rates of photosynthesis on 1- and 0.45-μm filters differed only by about 10%.

The difference in the type of incubator used for photosynthesis in 1980 and 1981 caused some problems. The maximum illumination possible with new fluorescent lights was 530 $\mu E \cdot m^{-2} \cdot s^{-1}$, compared with 1050 $\mu E \cdot m^{-2} \cdot s^{-1}$ with quartz–halogen lights. Moreover, the actual light intensity inside the bottle was different in the two incubators. In *Chlorella* cultures, values of α estimated in the 1980 incubator were 48.8% of the 1981 incubator values. Therefore, we applied this correction factor to all α values obtained during the three

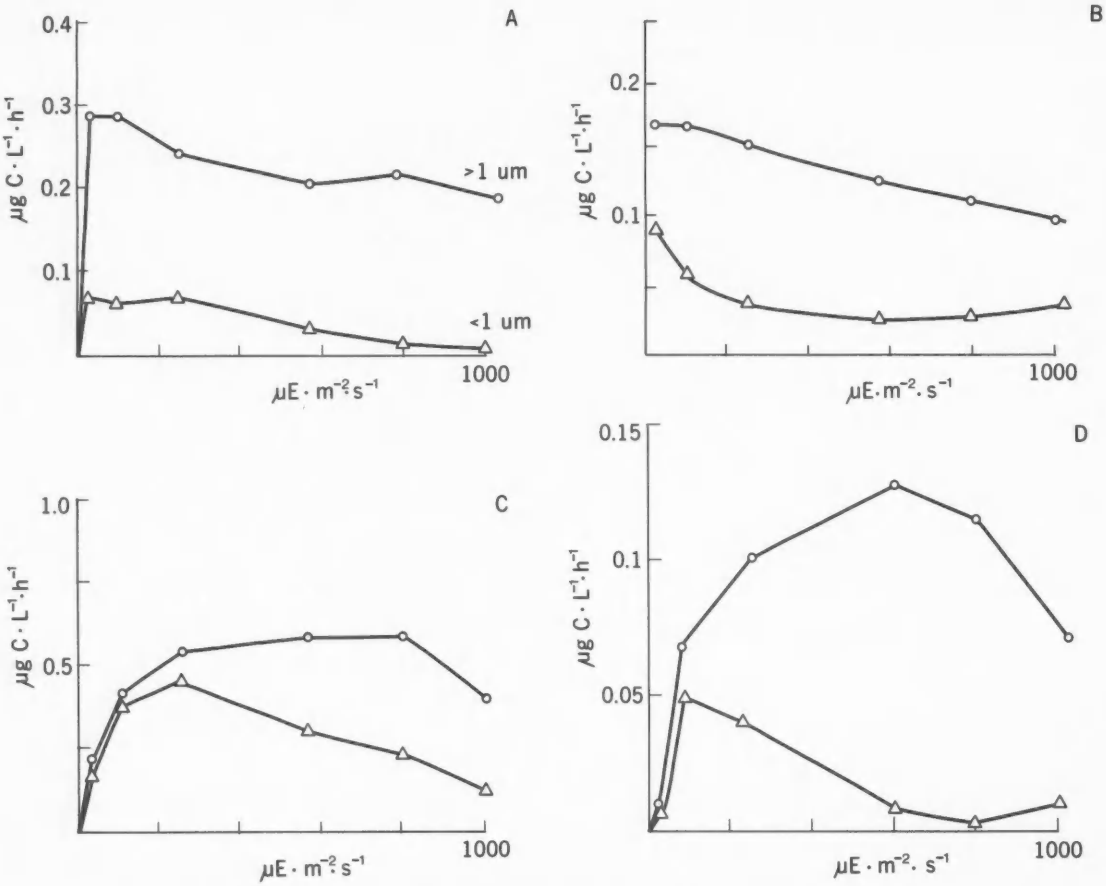

FIG. 2. Size-fractionation of ^{14}C uptake as a function of light intensity in organisms >1 μm and <1 μm (picoplankton).

cruises in 1980. In 11 of the 23 experiments carried out in 1980, P_{max} was not achieved, presumably because the maximal light intensity of 530 $\mu E \cdot m^{-2} \cdot s^{-1}$ at the bottom of the bottle in fact gave an effective intensity of only 260 $\mu E \cdot m^{-2} \cdot s^{-1}$ inside the bottle. However, in experiments carried out in 1981, P_{max} generally began at <200 $\mu E \cdot m^{-2} \cdot s^{-1}$; therefore, it is not likely that P_{max} in these 11 experiments from 1980 has been grossly underestimated.

In the whole data set, mean values of α did not differ significantly between inshore and offshore, between stratified and unstratified stations, or among seasons (Table 1). In 1981, light inhibition of photosynthesis began at lower intensities offshore than inshore and in isothermal compared with stratified waters. Seasonally, phytoplankton in the May–June period seemed low light adapted in contrast with the July phytoplankton. Inhibition of photosynthesis occurred between 100 and 315 $\mu E \cdot m^{-2} \cdot s^{-1}$ in May–June and 580–790 $\mu E \cdot m^{-2} \cdot s^{-1}$ in July. All stations sampled in May–June were unstratified, and growth rates in May–June were very similar to values during the isothermal period.

According to data on phosphate turnover time, stratified waters and inshore areas are more deficient in phosphorus than isothermal waters and offshore, respectively, but seasonal differences were not statistically significant (Table 1).

P_{max} to V_{max} (phosphate) ratios, proposed by Lean and Pick (1981) as an index of lake trophic status, were calculated on seven occasions, and three values were added from 1979 cruises (Nalewajko et al. 1981). The ratios ranged from 0.75 to 10.6, and showed a significant positive correlation ($P < 0.01$) with phosphate turnover time (Fig. 3). However, the clumping of data points at the lowest values of phosphate turnover time and absence of data in the 0.5–2.5 h range suggest that this relationship needs to be examined further.

A diurnal pattern of P_m^B was apparent (Fig. 4) when values were examined as a function of the time of day at which the experiments were started. Values were lowest during night and maximal around noon.

A stepwise multiple regression analysis was carried out for the entire data set to rank the contribution of the four variables (hours of sunshire in previous 3 d, temperature, phosphate turnover time, and time of day) to the observed variances of P_m^B. The analysis was repeated for inshore and offshore stations and for stratified and isothermal waters (Table 3). Temperature was ranked as the most important variable in the whole data set, as well as inshore, and at thermally stratified stations. However, offshore, and in isothermal waters, light history represented by hours of sunshine in the previous 3 d was more important than temperature.

TABLE 3. Stepwise multiple regressions of assimilation number and four variables

Group	% variance explained				
	By temp.	By h sunshine in previous 3 d	By phosphate turnover time (dark)	By time of day	By model
Whole data set	38.7	11.6	0.01	0.2	50.5%
Inshore	48.7	1.0	0.03	1.6	51.3
Offshore	23.77	54.2	0.4	11.8	90.1
Thermally stratified	34.6	9.8	13.8	0.4	58.6
Isothermal	0.6	73.3	8.4	5.3	87.5

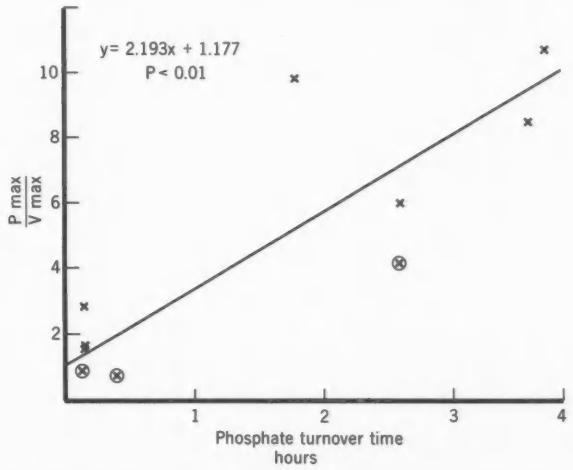

FIG. 3. P_{max}/V_{max} ratios and phosphate turnover time. On the three dates circled (from Nalewajko et al. 1981), P_{max} was not reached and values of carbon fixed at 260 $\mu E \cdot m^{-2} \cdot s^{-1}$ were used instead.

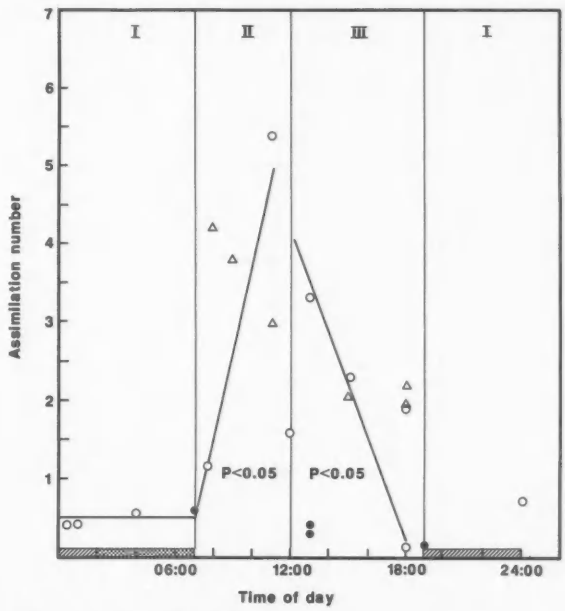

FIG. 4. Diurnal pattern of assimilation numbers. Periods: I, night; II, increasing solar radiation (approximate); III, decreasing solar radiation (approximate); ●, May–June; ○, July; △, October.

Phosphorus status estimated by phosphate turnover time was ranked second both in stratified and isothermal waters, but fourth in the other groups. Because the data sets are small, and the number of data points is not the same in each of the six groups, differences in the amount of variance explained in each group cannot be considered as significant. However, we suggest that ranking of the four variables within each group may yield additional insight into spatial and seasonal variation in the importance of environmental factors to phytoplankton production.

Discussion

Assimilation numbers in Lake Superior ranged from 0.1 to 5.0, with the exception of one station, near Duluth, Minnesota, where a value of 7.3 was obtained in July 1980. According to Curl and Small (1965), values between 0 and 3 indicate nutrient depletion, while 3–5 are borderline. P_m^B were not previously measured in Lake Superior, but Munawar et al. (1978) reported P/B ratios (daily light saturated photosynthetic rates normalized to unit phytoplankton biovolume) higher than in Lake Ontario or Lake Erie. This was attributed by the authors to a predominance of nannoplankton in Lake Superior. We have converted their data to P_m^B. Assuming a 12-h day, we calculated P_m^B values of 1.16 and 2.03 during unstratified and stratified periods, respectively, which is in agreement with values reported here (Table 1). The corresponding values in Lake Erie were 2.35 and 3.57. In Lake Huron, P_m^B values were low, 1.5–2, except in eutrophic Saginaw Bay and in an upwelling area near the Bruce Peninsula (Glooschenko et al. 1973). This trend of lower P_m^B in oligotrophic waters is similar to the results of Lastein and Gargas (1978), but the latter showed that the influence of temperature and light on P_m^B was stronger than the influence of lake trophic state. In agreement with Lastein and Gargas, Schelske et al. (1974) reported that nutrient enrichment did not change P_m^B in Lake Michigan and concluded that temperature had a more important influence than nutrients. Further, Glover (1980) reported large interspecific differences in P_m^B as a function of growth rate and nitrogen and iron availability and concluded that P_m^B values could not be used as indicators of nutrient status.

P_m^B depends on phytoplankton biomass and its physiological condition as determined by nutrient supply, light, and temperature. Indirect effects will be exerted by physical mixing

processes. Attempts to assess the relative contribution of different variables to P_m^B in natural ecosystems have depended on various statistical treatments including simple and partial correlation (Platt and Jassby 1976), linear regression (Lastein and Gargas 1978), and stepwise multiple regression (Harrison and Platt 1980). We chose to use this last technique to ascertain the percentage of variance in phytoplankton P_m^B attributable to temperature, light history, and phosphorus status and time of day. The ranking of temperature (Table 3) as the most important factor in the whole data set confirms the findings of Platt and Jassby (1976), Lastein and Gargas (1978), and Harrison and Platt (1980), among others. In agreement with Lastein and Gargas (1978), light history was the second most important variable, while phosphorus contributed very little.

The differences in the model outcome for inshore and offshore, and for stratified compared with isothermal stations, appear to confirm our hypothesis. The ranking of light history as the most important variable offshore and in isothermal waters suggests that the light regime imposed by the greater depth at offshore stations as well as the duration of isothermal mixing (Bennett 1978) may be the predominant factors affecting phytoplankton physiology. In contrast, inshore, and in stratified waters, temperature is a relatively more important factor. We suggest that offshore, and during isothermal mixing, P_m^B could be under the control of different environmental variables than inshore and during thermal stratification, without necessarily differing in numerical value. In Lake Superior the mean Z_m/Z_e ratio (Talling 1971) during isothermal mixing would be 8.42, but would decrease to about 1 once thermal stratification sets in. The seasonal increase in day length which is concomitant with onset of stratification would exacerbate the differences in the scales of variability in the light regime at stratified compared with isothermal stations.

Harris (1978) showed that phytoplankton adapt to the mean value of the ratio, that is to a mean light level, but suggested that the algae also respond to the amplitude, period, and phase of the variations of a given resource (Harris 1980), particularly if the resource availability frequently drops into or below the basal maintenance level (see Harris 1980, fig. 2). In Lake Superior, Langmuir circulation would allow phytoplankton to complete one "roll vortex" (Harris 1980) in the epilimnion in 4–6 h (F. Boyce, CCIW, pers. comm.), but it would require 40–60 h at an unstratified offshore station 200 m deep. Consequently, phytoplankton in the latter environment would experience surface light less frequently, and would spend longer periods of time in the dark, compared with epilimnetic phytoplankton. Higher chlorophyll *a* concentration per unit phytoplankton biovolume at isothermal (0.006) compared with stratified (0.0032) stations, the lower P_{max}, and the onset of light-inhibited photosynthesis at lower light intensities (Table 1) are symptoms of low-light-grown phytoplankton (Harris 1978). While the lower P_{max} could be, to a large extent, a result of the lower temperature at isothermal stations (Table 1), lower temperature would be expected to decrease chlorophyll per cell, or to have no effect (Harris 1978). We are not aware of published data on the effect of low growth temperature on the onset or extent of light-inhibited photosynthesis. In our experiments with phosphorus-sufficient *Chlorella* in semicontinuous culture there were no significant differences in light inhibition of photosynthesis between cultures grown at 12 and 22°C (C. Nalewajko, unpubl. data). Therefore, we suggest that the characteristics observed in phytoplankton from the isothermal stations are more likely to have developed in response to low light than to low temperature. Such an interpretation is consistent with the ranking of light history and temperature as the number one variables in isothermal and stratified waters, respectively.

The choice of 3-d light data as an estimate of light history was made following the report by Platt and Jassby (1976) that this time scale was appropriate for phytoplankton to respond, but subsequently, Harris (1978) and Côté and Platt (1983) pointed out that the physiological response of phytoplankton is close to the order of a generation time. Here, growth rate, as doublings per day, ranged from 0.15 to 0.65 (Table 1), (i.e. generation time ranged from 6.7 d (May–June) to 1.54 d (stratified waters). Therefore, the use of 3-d light data may represent a reasonable compromise.

A diurnal pattern of P_m^B, with lowest values at night and a maximum about midday, has been found in a variety of environments (Harris 1978). It may be accompanied by diel variations in α, or occur alone, as observed here. According to MacCaull and Platt (1977) the amplitude of the oscillations in P_m^B is sufficiently large to represent a significant error in estimates of primary production. In our data set the occurrence of a diurnal pattern in P_m^B was discovered a posteriori. It cannot be regarded as a systematic source of error because there are no significant differences in time-of-day values within groups A, B, and C (Table 1).

Correlations between assimilation number and temperature have been noted frequently both in freshwaters (Harris 1980) and in marine environments (Côté and Platt 1983). Such a correlation is to be expected in view of temperature dependence of P_{max}. The potential effects of light on P_m^B are less well documented. An exception is the work of Laws and Bannister (1980) who give P_m^B data as a function of growth rate of *Thalassiosira fluviatilis* during nutrient and light limitation. When growth was limited by light to 50% of P_{max}, P_m^B values were < 1, compared with about 5 when nitrogen or phosphorus limited growth to the same extent. The low P_m^B at isothermal stations (Table 1) coincident with long phosphate turnover time (i.e. with a period of relative phosphorus sufficiency) reinforces our interpretation that light is the limiting factor for phytoplankton growth at this time.

Phytoplankton growth rates have not been estimated previously in Lake Superior or in the other Upper Great Lakes. The lowest values, in May–June, are similar to the growth rates for *Cyclotella glomerata* calculated from the data of Schelske et al. (1972) for Lake Superior. On phosphate enrichment, the growth rate increased from 0.14 to 0.29 doublings$\cdot$d^{-1}, while enrichment with phosphorus, silica, nitrate, trace metals, and vitamins resulted in 0.70 doublings$\cdot$d^{-1}. Given the conflicting results on phytoplankton growth rates in oligotrophic versus eutrophic waters, and the lack of completely satisfactory techniques for making accurate estimates of in situ growth rates (Goldman et al. 1979), it is premature to comment further on the absolute values of these growth rate estimates. However, there are significant differences in phytoplankton growth rates at stratified compared with unstratified stations. Besides the differences in temperature and Z_m/Z_e discussed earlier, these areas differ significantly in phosphate turnover time.

The use of phosphate turnover time as an estimate of phosphorus availability was proposed by Lean and Nalewajko (1979) and is based on evidence that in cultures of algae, phosphate turnover time is responsive both to the cell phosphorus quota and to phosphate availability in the medium (Nalewajko and Lean 1978). Lean and Pick (1981) later proposed

a refined index, the P_{max}/V_{max} ratio. On that scale, values of <10 indicate extreme phosphorus deficiency, and 10–30 moderate deficiency. The significant positive correlation with P_{max}/V_{max} shown here suggests that dark phosphate turnover time, which is logistically a more convenient parameter to obtain, is as useful as the more complex ratio for estimating phosphorus states of lake water. From the P_{max}/V_{max} regression against phosphate turnover time (Fig. 3), and the mean values of phosphate turnover time (Table 1) in stratified and unstratified waters, we obtained P_{max}/V_{max} values of 4.7 and 26, respectively. These values suggest that phytoplankton in stratified waters is extremely phosphorus deficient but in unstratified waters only moderately deficient. Even with identical phosphorus loading, it is feasible that the higher light and higher temperature regime leads to higher growth rates and biomass in stratified waters, which results in a greater shortage of phosphorus than can develop under isothermal conditions over the same period.

Recent studies on the effects of temperature and light on algal growth rate as a function of nutrient supply (Rhee and Gotham 1981a, 1981b; Zevenboom 1980; Riegman 1985) have clearly demonstrated that at equivalent growth rates, cell quota of a given nutrient is higher when temperature or light, rather than a nutrient, limits growth. Minimum cell quotas appear to show similar trends. A higher cell phosphorus quota would lead to a decrease in the measured $^{32}P\text{-}PO_4$ influx, hence to a longer phosphate turnover time. Not only is there less phytoplankton at times of isothermal mixing, but each cell is also richer in phosphorus than phytoplankton from stratified waters; overall, the result is a much longer phosphate turnover time.

As expected in oligotrophic waters, and previously demonstrated by Munawar and Munawar (1978), seasonal variability of phytoplankton biovolume in Lake Superior was very limited. They reported also that the biovolume was lower than in the other Laurentian Great Lakes but similar to offshore Georgian Bay. Also, inshore–offshore differences were not as pronounced as in the Lower Great Lakes. Munawar and Munawar (1978) observed that biological differences between stratified and isothermal waters were larger than among seasons or between inshore and offshore areas. Our data (Table 1) confirm these conclusions.

Munawar et al. (1978) emphasized the greater importance of nannoplankton (defined as algae <64 μm) and phytoflagellates in Lake Superior relative to the other Laurentian Great Lakes, but did not detect any large differences in the contribution of any size group to total phytoplankton biomass in stratified compared with unstratified regions of Lake Superior (Munawar and Munawar 1978). This contrasts with our data (Table 2) which revealed a significantly higher contribution by the microalgae in isothermal than in stratified water.

Munawar et al. (1978) also estimated the contribution of various size-classes of phytoplankton to primary production, but the smallest size-class examined was <10 μm. Thus the presence of picoplankton, generally defined as <2 μm, would not have been detected. Following the original reports of picoplankton in the ocean (Waterbury et al. 1979; Johnson and Sieburth 1979), organisms of that size range have been shown to be ubiquitous in marine environments. Recently, cyanobacteria <1 μm were discovered in Lake Ontario (Caron et al. 1985). We found that in Lake Superior, algae <1 μm are important contributors to photosynthesis at low light intensities. In this respect they resemble the marine cyanobacteria in which photosynthesis and growth saturate at very low light intensities (Morris and Glover 1981). Their ability to function well in blue–green light (Wood 1985) is also a feature of potential significance in Lake Superior, since these are the predominant wavelengths near the bottom of the photic zone (Jerome et al. 1983).

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References

BENNETT, E. B. 1978. Characteristics of the thermal regime of Lake Superior. J. Great Lakes Res. 4: 310–319.

CARON, D. A., F. R. PICK, AND D. R. S. LEAN. 1985. Chroococcoid cyanobacteria in Lake Ontario: vertical and seasonal distribution during 1982. J. Physiol. 21: 171–175.

CÔTÉ, B., AND T. PLATT. 1983. Day-to-day variations in the spring–summer photosynthetic parameters of coastal marine phytoplankton. Limnol. Oceanogr. 28: 320–344.

CURL, H. JR., AND L. F. SMALL. 1965. Variations in the spring–summer photosynthetic parameters of coastal marine phytoplankton. Limnol. Oceanogr. 28: 320–344.

ENVIRONMENT CANADA 1979. Analytical methods manual. Inland Waters Directorate, Water Quality Branch, Ottawa, Ont.

GLOOSCHENKO, W. A., J. E. MOORE, AND R. A. VOLLENWEIDER. 1973. Chlorophyll *a* distribution in Lake Huron and its relationship to primary productivity. Proc. 16th Conf. Great Lakes Res. Int. Assoc. Great Lakes Res. 40–49.

GLOVER, H. E. 1980. Assimilation numbers in cultures of marine phytoplankton. J. Plankton Res. 2: 69–79.

GOLDMAN, J. C., J. J. MCCARTHY, AND D. G. PEAVEY. 1979. Growth rate influence on the chemical composition of phytoplankton in oceanic waters. Nature (Lond.) 279: 210–215.

HARRIS, G. P. 1978. Photosynthesis, productivity and growth; physiological ecology of phytoplankton. Arch. Hydrobiol. Beih. Ergeb. Limnol. 10: 1–171.

1980. Measurement of photosynthesis, p. 129–187. *In* I. Morris [ed.] Physiological ecology of phytoplankton. Blackwell Scientific Publications, Oxford.

HARRISON, W. G., AND T. PLATT. 1980. Variations in assimilation number of coastal marine phytoplankton: effects of environmental co-variates. J. Plankton Res. 2: 249–260.

INTERNATIONAL JOINT COMMISSION UPPER LAKES REFERENCE GROUP. 1977. The waters of Lake Huron and Lake Superior. Vol. III, Part B. Lake Superior. p. 332–350.

JEROME, J. H., R. P. BUKATA, AND J. E. BURTON. 1983. Spectral attenuation and irradiance in the Laurentian Great Lakes. J. Great Lakes Res. 9: 60–68.

JOHNSON, P. W., AND J. MCN. SIEBURTH. 1979. Chroococcoid cyanobacteria in the sea: a ubiquitous biomass. Limnol. Oceanogr. 24: 928–935.

LASTEIN, E., AND E. GARGAS. 1978. Relationship between phytoplankton photosynthesis and light, temperature and nutrients in shallow lakes. Verh. Int. Ver. Limnol. 20: 678–689.

LAWS, E. A., AND T. T. BANNISTER. 1980. Nutrient- and light-limited growth of *Thalassiosira fluviatilis* in continuous culture, with implications for phytoplankton growth in the ocean. Limnol. Oceanogr. 25: 457–473.

LEAN, D. R. S., AND C. NALEWAJKO. 1979. Phosphorus turnover time and phosphorus demand in large and small lakes. Arch. Hydrobiol. Beih. Ergeb. Limnol. 13: 120–132.

LEAN, D. R. S., AND F. R. PICK. 1981. Photosynthetic response of lake plankton to nutrient enrichment: a test for nutrient limitation. Limnol. Oceanogr. 26: 1001–1019.

MACCAULL, W. A., AND T. PLATT. 1977. Diel variations in the photosynthetic parameters of coastal marine phytoplankton. Limnol. Oceanogr. 22: 723–731.

MORRIS, I., AND H. GLOVER. 1981. Physiology of photosynthesis by marine coccoid cyanobacteria — some ecological implications. Limnol. Oceanogr. 26: 957–961.

MUNAWAR, M., AND I. F. MUNAWAR. 1978. Phytoplankton of Lake Superior

1973. J. Great Lakes Res. 4: 415–442.

MUNAWAR, M., I. F. MUNAWAR, L. R. CULP, AND G. DUPUIS. 1978. Relative importance of nannoplankton in Lake Superior phytoplankton biomass and community metabolism. J. Great Lakes Res. 4: 462–480.

NALEWAJKO, C., AND D. R. S. LEAN. 1978. Phosphorus kinetics – Algal growth relationships in batch cultures. Mitt. Int. Ver. Limnol. 21: 184–192.

NALEWAJKO, C., K. LEE, AND H. SHEAR. 1981. Phosphorus kinetics in Lake Superior: light intensity and phosphate uptake in algae. Can. J. Fish. Aquat. Sci. 38: 224–232.

NALEWAJKO, C., B. PAUL, K. LEE, AND H. SHEAR. 1986. Light history, phosphorus status, and the occurrence of light stimulation or inhibition of phosphate uptake in Lake Superior phytoplankton and bacteria. Can. J. Fish. Aquat. Sci. 43: 329–335.

PLATT, T., AND A. D. JASSBY. 1976. The relationship between photosynthesis and light for natural assemblages of coastal marine phytoplankton. J. Phycol. 12: 421–430.

RHEE, G-Y., AND I. J. GOTHAM. 1981a. The effect of environmental factors on phytoplankton growth: temperature and the interaction of temperature with nutrient limitation. Limnol. Oceanogr. 26: 635–648.

1981b. The effect of environmental factors on phytoplankton growth: light and the interactions of light with nitrate limitation. Limnol. Oceanogr. 26: 649–659.

RIEGMAN, R. 1985. Phosphate–phytoplankton interactions. Doctoral thesis, University of Amsterdam, Amsterdam, The Netherlands. 143 p.

SCHELSKE, C. L., AND E. CALLENDER. 1970. Survey of phytoplankton productivity and nutrients in Lake Michigan and Lake Superior. Proc. 13th Conf. Great Lakes Res. Int. Assoc. Great Lakes Res. 149–165.

SCHELSKE, C. L., E. FELDT, M. A. SANTIAGO, AND E. F. STOERMER. 1972. Nutrient enrichment and its effect on phytoplankton production and species composition in Lake Superior. Proc. 15th Conf. Great Lakes Res. Int. Assoc. Great Lakes Res. 149–165.

SCHELSKE, C. L., E. D. ROTHMAN, E. F. STOERMER, AND M. A. SANTIAGO. 1974. Responses of phosphorus limited Lake Michigan phytoplankton to factorial enrichment with nitrogen and phosphorus. Limnol. Oceanogr. 19: 409–419.

SCHINDLER, D. W. 1974. Eutrophication and recovery in Experimental Lakes: implications for lake management. Science (Wash., DC) 184: 897–898.

SHEAR, H., K. LEE, AND C. NALEWAJKO. 1981. A seasonal survey of phosphorus kinetics in Great Lakes phytoplankton. Poster, 44th Annual Meeting, American Society of Limnology and Oceanography, Milwaukee, WI.

TALLING, J. F. 1971. The underwater light climate as a controlling factor in the production ecology of freshwater phytoplankton. Mitt. Int. Ver. Theor. Angew. Limnol. 19: 214–243.

WATERBURY, J. B., S. W. WATSON, R. R. L. GUILLARD, AND L. E. BRAND. 1979. Widespread occurrence of a unicellular, marine, planktonic, cyanobacterium. Nature (Lond.) 277: 293–294.

WOOD, A. M. 1985. Adaptation of photosynthetic apparatus of marine ultraphytoplankton to natural light fields. Nature (London.) 316: 253–255.

ZEVENBOOM, W. 1980. Growth and nutrient uptake kinetics of *Oscillatoria agardhii*. Doctoral thesis, University of Amsterdam, Amsterdam, The Netherlands. 178 p.

Experimental Study of the Impacts of Bluegill (*Lepomis macrochirus*) and Largemouth Bass (*Micropterus salmoides*) on Pond Community Structure

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Hambright, K. D., R. J. Trebatoski, R. W. Drenner, and D. Kettle. 1986. Experimental study of the impacts of bluegill (*Lepomis macrochirus*) and largemouth bass (*Micropterus salmoides*) on pond community structure. Can. J. Fish. Aquat. Sci. 43: 1171–1176.

We examined community impacts of bluegill (*Lepomis macrochirus*) and largemouth bass (*Micropterus salmoides*) in a summer experimental pond study of factorial design with four treatment combinations (fishless, bluegill, largemouth bass, and bluegill with largemouth bass). *Ceriodaphnia reticulata*, *Daphnia pulicaria*, *Chaoborus* sp., *Volvox* sp., anisopteran and zygopteran nymphs, and dissolved oxygen levels were suppressed in the presence of bluegill. *Diaptomus* sp., *Conochiloides* sp., *Cyclotella* sp., *Navicula* sp., *Oocystis* sp., *Anabaena* sp., *Ceratium* sp., algal fluorescence, turbidity, 5- to 12.7-μm particles, and total phosphorus and total nitrogen were enhanced in the presence of bluegill. *Daphnia pulicaria* was enhanced and *Cyclotella* sp. and *Oocystis* sp. were suppressed in the presence of largemouth bass. Although the effects of the two fish were not independent, as indicated by significant bluegill × largemouth bass interactions for some plankton taxa, we found little evidence of bluegill impacts being reversed by largemouth bass. While total bluegill biomass was reduced and bluegill biomass distributions were shifted toward larger individuals, bluegill remained abundant in the presence of largemouth bass.

Nous avons examiné les répercussions qu'ont sur la communauté les crapets arlequins (*Lepomis macrochirus*) et les achigans à grande bouche (*Micropterus salmoides*) au cours d'une étude expérimentale réalisée pendant l'été dans un étang suivant un plan factoriel avec quatre combinaisons de traitement (sans poisson, crapet arlequin, achigan à grande bouche et crapet arlequin avec achigan à grande bouche). En présence de crapets arlequins, les concentrations d'oxygène dissous et le nombre de nymphes d'anisoptères et de zygoptères, de *Ceriodaphnia reticulata*, de *Daphnia pulicaria*, de *Chaoborus* sp. et de *Volvox* sp. ont diminué. Par contre, en leur présence, il y a eu augmentation du nombre de *Diaptomus* sp., de *Conochiloides* sp., de *Cyclotella* sp., de *Navicula* sp., d'*Oocystis* sp., d'*Anabaena* sp., de *Ceratium* sp., augmentation de la fluorescence des algues, de la turbidité, des particules d'un diamètre variant de 5 à 12,7 μm ainsi que du phosphore et de l'azote totaux. En présence d'achigans à grande bouche, le nombre de *D. pulicaria* a augmenté tandis que celui de *Cyclotella* sp. et d'*Oocystis* sp. a diminué. Bien que les effets des deux espèces de poisson n'étaient pas indépendants, tel qu'indiqué par les interactions importantes entre le crapet arlequin et l'achigan à grande bouche relativement à certains taxons de plancton, nous avons trouvé peu d'indications qui laissent croire que les répercussions des crapets arlequins soient renversées par les achigans à grande bouche. Bien que la biomasse totale de crapets arlequins ait diminué et que la répartition de leur biomasse se soit déplacée vers des individus plus gros, les crapets arlequins sont restés nombreux en présence d'achigans à grande bouche.

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Most experimental studies examining community impacts of fish have focused on planktivorous fish which are internal regulators of plankton community structure of lakes (Zaret 1980; Hurlbert and Mulla 1981). While piscivorous fish are top level consumers in most lakes and may affect plankton communities through predation on planktivorous fish, few workers have examined whether planktivore impacts are influenced by piscivory (Zaret and Paine 1973; Benndorf et al. 1984; Shapiro and Wright 1984; Spencer and King 1984). These studies show that the reduction of planktivore populations by piscivores results in a reversal or decline in intensity of planktivore effects. In this paper, we present results from an experimental pond study examining summer plankton community responses to planktivorous bluegill (*Lepomis macrochirus*) in the presence and absence of piscivorous largemouth bass (*Micropterus salmoides*). We show that suppression of large zooplankton and enhancement of phytoplankton by bluegill are not significantly reversed in the presence of largemouth bass.

Materials and Methods

The study was conducted at the University of Kansas Nelson Environmental Study Area (NESA) from 5 June to

30 September 1983, in two mud-bottomed ponds, each divided by concrete partitions into four 0.006-ha, 61-m^3 quadrants (approximately 6.0 × 7.0 × 1.4 m). A 2 × 2 factorial design (presence and absence of bluegill × presence and absence of largemouth bass) resulted in four treatment combinations: (1) fishless, (2) bluegill, (3) largemouth bass, and (4) bluegill with largemouth bass. Each treatment combination was replicated twice and assigned to quadrants using a randomized block design.

Before the experiment, macrophytes (primarily *Typha* sp. and *Salix* sp.) were removed from the ponds. To provide similar initial sediment and water chemistry in the ponds, each was alternately filled with well water, mixed by wading to suspend sediments, and then partially emptied into the other pond via underground plumbing. Both ponds were then drained and a 3.7 × 7.6 m plastic sheet placed over the central portion (approximately 50%) of each quadrant bottom to prevent excessive macrophytic growth. The uncovered areas of each quadrant were recolonized by macrophytes during the study. Ponds were filled with water from a fishless reservoir on 4–5 June (17:00–09:00). Water temperature was initially 20°C and increased to 29°C by August. The ponds did not stratify.

Fish were collected from Potter's Lake and West Campus Pond on the University of Kansas campus, a pond at NESA, and two ponds located approximately 24 km southwest of Lawrence. Fish were collected by either shoreline-seining or hook and line and transferred to NESA holding ponds for 2 wk prior to stocking. Bluegills (135–144 individuals/quadrant) were stocked on 23 June and largemouth bass (3 individuals/quadrant) on 24 June at 280 and 112 kg/ha, respectively, which are standing crops typically found in Kansas ponds (D. Gablehouse, Kansas Fish and Game Commission, pers. comm.). We apportioned fish biomass into three size classes of bluegill (small, intermediate, and large) and two size classes of largemouth bass (small and large) to mimic mean biomass frequency distributions which we calculated for 26 balanced bluegill/largemouth bass communities presented in Swingle (1950) (Fig. 1). Swingle characterized balanced communities as having (1) ratios of total forage fish biomass to total piscivorous fish biomass (F/C) ranging from 1.4 to 10.0, (2) ratios of small forage fish biomass to total piscivorous fish biomass (Y/C) ranging from 0.02 to 5.0, (3) more than 40% of the total fish biomass in the form of harvestable fish (A_T value), and (4) at least 18%, but preferably more than 35%, of the total bluegill biomass in the form of harvestable bluegills (A_F value). He defined small bluegills as those with body depths less than the mean piscivore mouth width. Intermediate bluegills have body depths greater than the mean piscivore mouth width, but are too small for angler harvest. Large bluegills also have body depths greater than the mean piscivore mouth width, but are large enough for angler harvest. Large and small largemouth bass are those which can and cannot be harvested by anglers. In our study the size ranges of small, intermediate, and large bluegills were 30–89, 90–127, and 128–203 mm total length (TL) and of small and large largemouth bass were 178–234 and 235–320 mm TL, respectively. Our ponds met Swingle's criteria for balance at the beginning and end of the experiment as shown by F/C values of 2.87 ± 0.13 and 2.65 ± 0.17, Y/C values of 1.04 ± 0.04 and 0.69 ± 0.10, A_T values of 0.66 and 0.69 ± 0.02, and A_F values of 0.58 ± 0.01 and 0.59 ± 0.05, respectively. Although bluegills spawned in all quadrants and largemouth bass did not, the fish communities remained balanced at pond drainage due to largemouth bass growth.

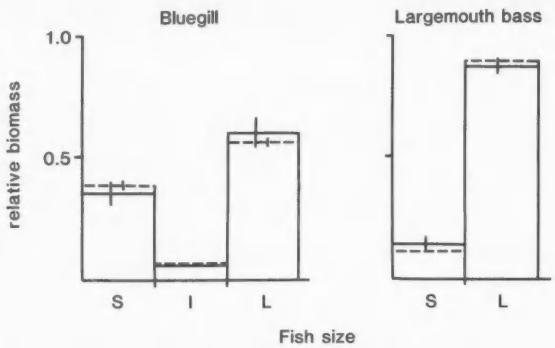

FIG. 1. Comparison of biomass frequency distributions of bluegill and largemouth bass stocked in pond quadrants (solid line) with biomass distributions in balanced bluegill/largemouth bass pond communities (Swingle 1950) (broken line). S = small, I = intermediate, and L = large. Vertical bars represent ± 1 SE.

On 30 September, fish and bullfrog tadpoles (*Rana catesbieana*) were recovered by rotenone poisoning. After rotenoning, ponds were checked for 1 wk to ensure recovery of all fish and tadpoles. One largemouth bass was not recovered and another was recovered from a bluegill quadrant. Because largemouth bass were last observed to be in proper quadrants on 5 August, we have limited our analyses to the period 5 June – 5 August.

Beginning on 5 June, zooplankton were sampled every 10 d between 22:00 and 02:00. Two samples were taken from each quadrant by vertical tows of a 63-μm-mesh conical plankton net (29.5-cm diameter) and preserved in 5% sucrose–formalin. Zooplankters were counted from 1-mL subsamples until the standard deviation of each count fell within 10% of the mean for each taxon. Zooplankters were identified according to Pennak (1953), Edmondson (1959), and Ruttner-Kolisko (1974). Phytoplankton were sampled between 08:00 and 10:00 on three days prior to fish stocking (5, 13, 19 June) and on four days after stocking (25 June, 5, 15, 27 July). Nannoplankton were collected using a deNoyelles' integrated phytoplankton sampler (deNoyelles and O'Brien 1978) which quantitatively samples the water column. The contents of the sampler were discharged into a plastic container, mixed, and subsampled (two 125-mL aliquots). Each quadrant was sampled twice, resulting in four 125-mL subsamples. Two subsamples were preserved in 1% Lugol's solution and two were used to determine algal fluorescence (Turner model 10 Rackmount Fluorometer), turbidity (HACH Turbidimeter), and particle densities (model ZB Coulter Counter, 100-μm aperature tube).

After thorough mixing, volumes (5, 10, or 25 mL) of the preserved subsamples were placed into sedimentation chambers using a large-orifice pipette and allowed to settle overnight (Sournia 1978). The volume settled was selected to provide a density ≥2 algal cells per field. After settling, the supernatant was removed and a coverglass placed over the bottom chamber. Twenty-five fields were counted along 10 transects using a Wild M40 phase contrast inverted microscope. The chamber was then turned 90° and an additional 25 fields counted. Net phytoplankton were counted in a similar manner but using 1-mL subsamples from the zooplankton samples. Identifications were made according to Prescott (1962, 1970) and Whitford and Schumacher (1973).

Alkalinity (potentiometric titration, APHA 1980), pH

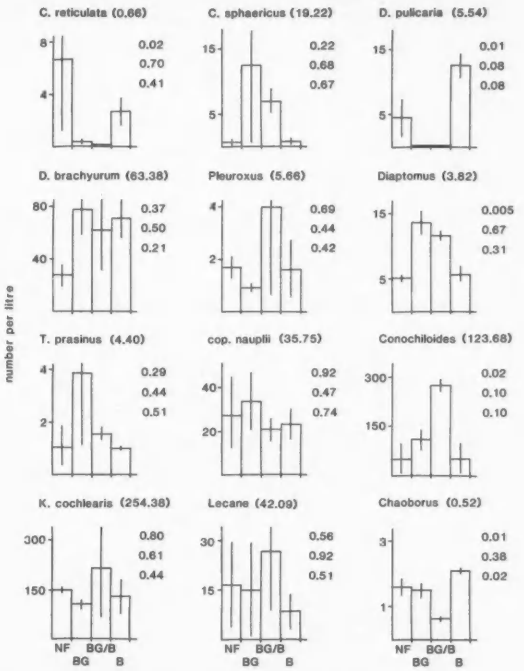

FIG. 2. Mean number of zooplankters per litre after fish stocking (24 June − 5 August) in fishless (NF), bluegill (BG), bluegill/largemouth bass (BG/B), and largemouth bass (B) treatment combinations. Probability values for bluegill (upper) and largemouth bass (middle) main effects and interactions (lower) are given to the right of each histogram. Vertical bars represent ± 1 SE. $\sqrt{MS_{error}}$ shown in parentheses.

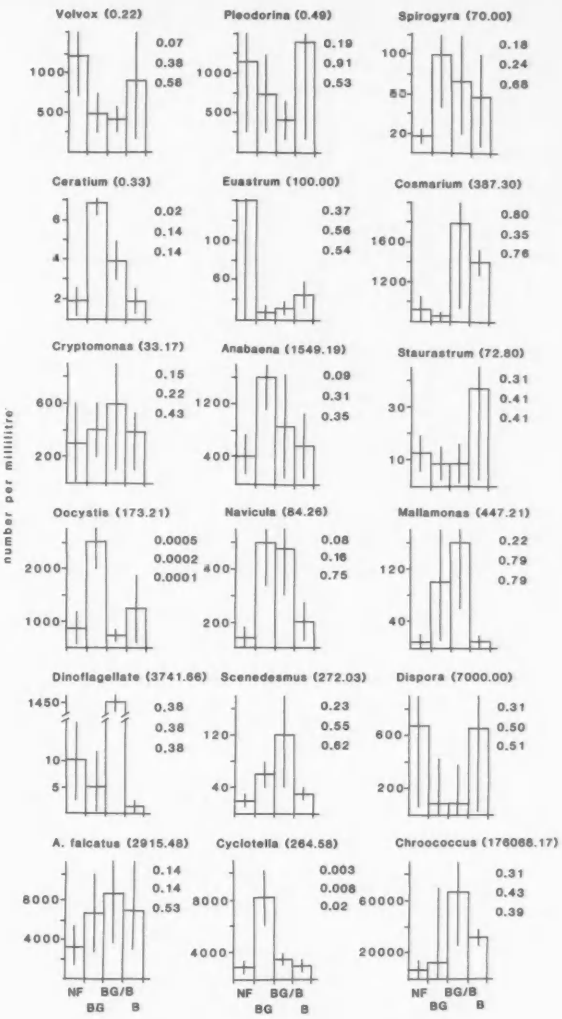

FIG. 3. Mean number of phytoplankton per millilitre after fish stocking (24 June − 27 July) in fishless (NF), bluegill (BG), bluegill/largemouth bass (BG/B), and largemouth bass (B) treatment combinations. Probability values for bluegill (upper) and largemouth bass (middle) main effects and interactions (lower) are given to the right of each histogram. Vertical bars represent ± 1 SE. $\sqrt{MS_{error}}$ shown in parentheses.

(Sargent−Welch pH meter), and dissolved oxygen (YSI meter and Winkler Titration, APHA 1980) were measured on each sampling date. On 5, 9, and 10 June, 11, 13, and 17 July, and 30 September, additional water samples were frozen for analysis of total phosphorus (TP) and total nitrogen (TN). Two 25-mL samples were analyzed from each quadrant on each sampling date. Samples for TP were digested with potassium persulfate (Menzel and Corwin 1965) and analyzed by a modification of the ascorbic acid method (APHA 1980) in which 4 mL of color reagent was added to 25-mL samples and read at 665 nm (D. Wright, Limnological Research Center, University of Minnesota, Minneapolis, MN, pers. comm.). Samples for TN were digested with alkaline potassium persulfate (D'Elia et al. 1977) and analyzed using the UV absorption method (APHA 1980).

Macroinvertebrates (primarily anisopteran and zygopteran nymphs; Order Odonata) were sampled on 14, 22, and 28 July and 5 August between 22:00 and 02:00 with a 63-μm-mesh conical plankton net (19.5-cm diameter). The net, attached to a pole, was pushed through the macrophytic vegetation along the length of the concrete partitions in each quadrant 0.75 m below the water surface. Samples were preserved in 5% sucrose−formalin, and all odonate nymphs were counted and identified using Pennak (1953).

Sampling of ponds produced time series data which were analyzed by a split-plot ANOVA with repeated measures on one factor. This ANOVA accounts for the autocorrelation of pond samples through time (Winer 1971; Gill 1978). The analysis generates three effects terms: main effects, interactions, and simple effects. Main effects allow independent assessments of the impact of each factor (bluegill and largemouth bass), interactions allow assessment of the interdependence among factors, and simple effects allow for a further examination of interactions through direct comparison of treatment combinations. To evaluate variability between quadrants prior to fish introduction, quadrants were paired as if fish were present.

A past study at NESA involved fertilization of one of the experimental ponds and may have contributed to variation between treatment replicates. A preliminary test on the model was performed at $\alpha = 0.25$ to remove confounding pond

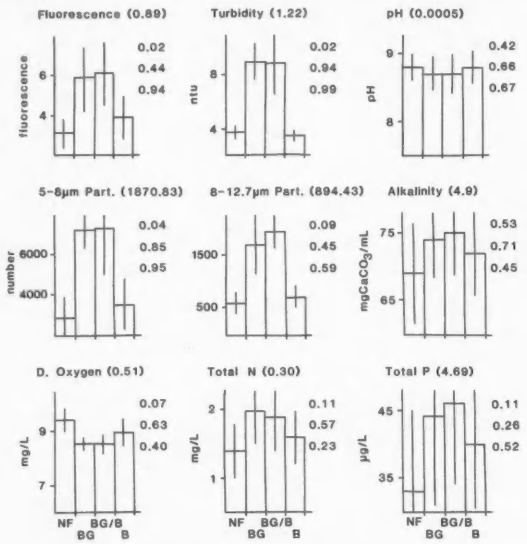

FIG. 4. Mean levels of algal fluorescence, turbidity, electronically counted particles, and water chemistry parameters after fish stocking (24 June – 27 July) in fishless (NF), bluegill (BG), bluegill/largemouth bass (BG/B), and largemouth bass (B) treatment combinations. Probability values for bluegill (upper) and largemouth bass (middle) main effects and interactions (lower) are given to the right of each histogram. Vertical bars represent ± 1 SE. $\sqrt{MS_{error}}$ shown in parentheses.

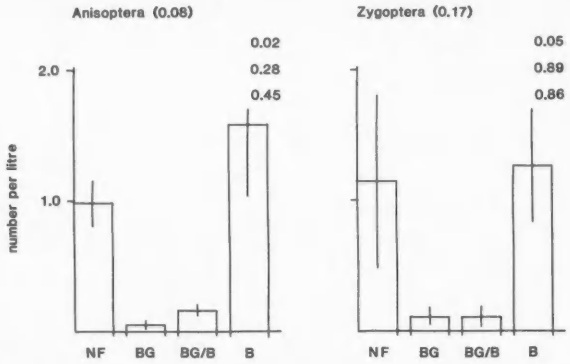

FIG. 5. Mean number of anisopteran and zygopteran (Order Odonata) nymphs per litre after fish stocking (24 June – 5 August) in fishless (NF), bluegill (BG), bluegill/largemouth bass (BG/B), and largemouth bass (B) treatment combinations. Probability values for bluegill (upper) and largemouth bass (middle) main effects and interactions (lower) are given. Vertical bars represent ± 1 SE. $\sqrt{MS_{error}}$ shown in parentheses.

(block) effects (Sokal and Rohlf 1969; Winer 1971). All significant pond effects ($\alpha \leq 0.25$) were dropped and the remaining sums of squares and degrees of freedom pooled to calculate a residual MS error term (Sokal and Rohlf 1969). Alpha was set at 0.25 to reduce the chance of committing a type II error (β) (Winer 1971). The experimental design and twofold replication resulted in low sensitivity for determining bluegill × largemouth bass interactions. The experiment was capable of detecting bluegill × largemouth bass interactions $\geq 2.6\sqrt{MS_{error}}$ at $\alpha = 0.10$, with $\beta \leq 0.10$.

Results

Ceriodaphnia reticulata, *Daphnia pulicaria*, *Chaoborus* sp., *Volvox* sp., and zygopteran and anisopteran nymphs were less abundant in the presence of bluegill (Fig. 2, 3, and 5). *Diaptomus* sp., *Conochiloides* sp., *Cyclotella* sp., *Navicula* sp., *Oocystis* sp., *Anabaena* sp., *Ceratium* sp., algal fluorescence, turbidity, and 5- to 8-µm and 8- to 12.7-µm particles were higher in quadrants with bluegill (Fig. 2, 3, and 4). TP and TN were higher and dissolved oxygen was lower in treatments with bluegill (Fig. 4). Largemouth bass had no effects on odonate nymphs or water chemistry but were associated with a higher abundance of *D. pulicaria* and lower abundances of *Cyclotella* sp. and *Oocystis* sp. (Fig. 2 and 3). Significant bluegill × largemouth bass interactions were detected for *Chaoborus* sp., *D. pulicaria*, *Conochiloides* sp., *Cyclotella* sp., and *Oocystis* sp. (Fig. 2 and 3). Analysis of these interactions by simple effects indicates that *Chaoborus* sp., *Cyclotella* sp., and *Oocystis* sp. were significantly less abundant ($P = 0.02$, 0.004, and 0.01, respectively) in bluegill/largemouth bass quadrants relative to bluegill quadrants. *Conochiloides* sp. were higher in abundance in bluegill/largemouth bass quadrants relative to bluegill quadrants ($P = 0.04$). In bluegill/largemouth bass quadrants, *D. pulicaria* decreased in abundance relative to bass quadrants ($P = 0.009$), but were similar ($P = 0.86$) to those in bluegill quadrants. None of these main or interaction effects were detected prior to fish introduction.

TABLE 1. Bluegill biomass stocked and recovered in replicates a and b of bluegill (BG) and bluegill/largemouth bass (BG/B) treatment combinations.

		Biomass (g)	
		Stocked	Recovered
BG	a	1812.7	1934.0
	b	1502.4	2152.3
BG/B	a	1880.2	1865.6
	b	1783.0	1655.2

Recovery data of fish on 30 September showed that bluegill biomass in bluegill/largemouth bass quadrants was approximately 15% lower relative to bluegill quadrants (Table 1). While bluegill biomass distributions were shifted toward the larger size class (Fig. 6), 33 and 41% of the bluegill biomass was small enough to be consumed by the largest bass in each bluegill/largemouth bass quadrant. Tadpole biomass was highest in quadrants with only bluegill and lower in quadrants containing largemouth bass (Fig. 7).

Discussion

Bluegill typically suppress populations of large-bodied zooplankters and odonates, but enhance populations of phytoplankton and small-bodied and highly evasive zooplankton and nutrient levels (Hall et al. 1970; Werner and Hall 1976; Bartell 1982; Lynch and Shapiro 1981; Crowder and Cooper 1982; Morin 1984). Phytoplankton increases have been attributed to changes in zooplankton community structure or alteration of nutrient cycles (Lamarra 1975; Hurlbert and Mulla 1981).

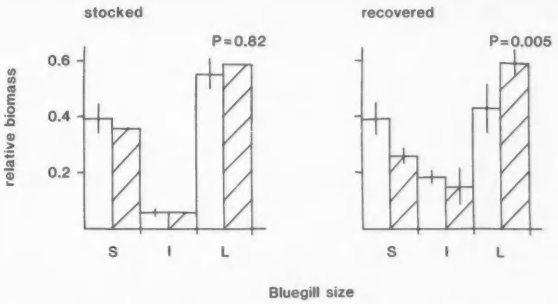

FIG. 6. Bluegill biomass distributions stocked and recovered in bluegill (open bars) and bluegill/largemouth bass (hatched bars) treatment combinations and the results of a chi-squared analysis. S = small, I = intermediate, and L = large. Vertical bars represent ± 1 SE.

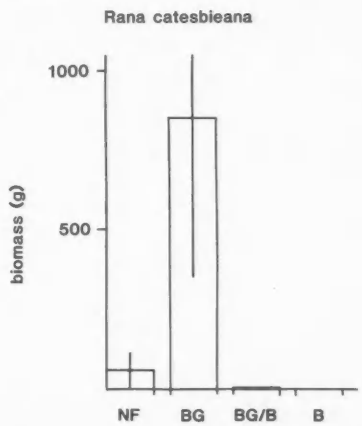

FIG. 7. Mean tadpole (*Rana catesbieana*) biomass recovered from fishless (NF), bluegill (BG), bluegill/largemouth bass (BG/B), and largemouth bass (B) treatment combinations. Vertical bars represent the range between replicates.

Because bluegill suppressed large herbivorous zooplankton and increased phosphorus and nitrogen levels, we cannot discriminate between these two alternative mechanisms. Although tadpoles are algal grazers and can suppress phytoplankton populations (Dickman 1968; Seale 1980), tadpole effects on phytoplankton were not apparent. Bluegill enhancement of phytoplankton was similar in both the presence and absence of tadpoles.

While significant interactions between largemouth bass and bluegill indicate that some of the impacts of the two fish were not independent, we found little evidence of bluegill impacts being reversed by largemouth bass. Piscivores can affect planktivores either by causing a change in planktivore feeding habits or by reducing the planktivore populations. Werner et al. (1983) found that the presence of largemouth bass was correlated with a delay in shift of feeding habitat from the littoral to the pelagic zone by young bluegill. We did not examine bluegill habitat choice. However, the small size of the ponds may not have permitted a habitat shift by bluegill.

Studies showing a reduction of planktivore biomass by piscivores (Zaret and Paine 1973; Benndorf et al. 1984; Spencer and King 1984) involved minnow-like planktivores which are highly vulnerable to piscivory because of their small size. Bluegill are deep bodied and can grow to a size not available to largemouth bass, providing adult bluegill a size refugium from largemouth bass predation (Lawrence 1957; Werner et al. 1983). However, Shapiro and Wright (1984) showed that piscivores can reverse bluegill impacts on plankton communities and nutrients if fish are stocked in a high piscivore to planktivore ratio.

Although the low replication, short duration of the study, and failure of largemouth bass to reproduce limited our ability to detect largemouth bass effects on the plankton community response to bluegill, our study suggests that bluegill effects may not be reversed by largemouth bass when the fish populations occur at natural standing crops. Because they have coevolved with largemouth bass and have behavioral and physical characteristics which reduce their vulnerability to piscivory (Howick and O'Brien 1983), bluegills are typically abundant in lakes containing largemouth bass (Cooper et al. 1971; Carlander 1977).

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References

AMERICAN PUBLIC HEALTH ASSOCIATION (APHA). 1980. Standard methods for the examination of water and waste water. 15th ed. APHA, Washington, DC.

BARTELL, S. M. 1982. Influence of prey abundance on size-selective predation by bluegills. Trans. Am. Fish. Soc. 111: 453–461.

BENNDORF, J., H. KNESCHKE, K. KOSSATZ, AND E. PENZ. 1984. Manipulation of the pelagic food web by stocking with predacious fishes. Int. Rev. Gesamten Hydrobiol. 69: 407–428.

CARLANDER, K. D. 1977. Handbook of freshwater fishery biology. Volume 2. Life history data on centrarchid fishes of the United States and Canada. Iowa State University Press, Ames, IA.

COOPER, E. L., C. C. WAGNER, AND G. E. KRANTZ. 1971. Bluegills dominate the production in mixed populations of fishes. Ecology 52: 280–290.

CROWDER, L. B., AND W. E. COOPER. 1982. Habitat structural complexity and the interaction between bluegills and their prey. Ecology 63: 1802–1813.

D'ELIA, C. F., P. A. STEUDLER, AND N. CORWIN. 1977. Determination of total nitrogen in aqueous samples using persulfate digestion. Limnol. Oceanogr. 22: 760–764.

DENOYELLES, F. J., AND W. J. O'BRIEN. 1978. Phytoplankton succession in nutrient enriched experimental ponds as related to changing carbon, nitrogen and phosphorus conditions. Arch. Hydrobiol. 84: 137–165.

DICKMAN, M. 1968. The effect of grazing by tadpoles on the structure of a periphyton community. Ecology 49: 1188–1190.

EDMONDSON, W. T. [ED.] 1959. Freshwater biology. John Wiley & Sons, Inc., New York, NY.

GILL, J. L. 1978. Design and analysis of experiments in the animal and medical sciences. Iowa State University Press, Ames, IA.

HALL, D. J., W. E. COOPER, AND E. E. WERNER. 1970. An experimental approach to the production dynamics and structure of freshwater animal communities. Limnol. Oceanogr. 15: 839–928.

HOWICK, G. L., AND W. J. O'BRIEN. 1983. Piscivorous feeding behavior of largemouth bass: an experimental analysis. Trans. Am. Fish. Soc. 112: 508–516.

HURLBERT, S. H., AND M. S. MULLA. 1981. Impacts of mosquitofish (*Gambusia affinis*) predation on plankton communities. Hydrobiologia 83: 125–151.

LAMARRA, V. A. 1975. Digestive activities of carp as a major contributor to the nutrient loading in lakes. Verh. Int. Ver. Limnol. 19: 2461–2468.

LAWRENCE, J. M. 1957. Estimated sizes of various forage fishes largemouth

bass can swallow. Proc. Annu. Conf. Southeast. Assoc. Game Fish Comm. 11: 220–225.

LYNCH, M., AND J. SHAPIRO. 1981. Predation, enrichment and phytoplankton community structure. Limnol. Oceanogr. 26: 86–102.

MENZEL, D. W., AND N. CORWIN. 1965. The measurement of total phosphorus in seawater based on the liberation of organically bound fractions by persulphate oxidation. Limnol. Oceanogr. 10: 280–282.

MORIN, P. J. 1984. The impact of fish exclusion on the abundance and species composition of larval odonates: results of short-term experiments in a North Carolina farm pond. Ecology 65: 53–60.

PENNAK, R. W. 1953. Freshwater invertebrates of the United States. Ronald Press Company, New York, NY.

PRESCOTT, G. W. 1962. Algae of the western Great Lakes area. Wm. C. Brown Co. Publishers, Dubuque, IA.

1970. How to know the freshwater algae. Wm. C. Brown Co. Publishers, Dubuque, IA.

RUTTNER-KOLISKO, A. 1974. Plankton rotifers: biology and taxonomy. Die Binnengewasser. Einzeldarsellungen aus der limnologie und ihren nachbargebreten. Part 1. English translation by G. Kolisko.

SEALE, D. B. 1980. The influences of amphibian larvae on primary production, nutrient flux, and competition in a pond ecosystem. Ecology 61: 1531–1550.

SHAPIRO, J., AND D. I. WRIGHT. 1984. Lake restoration by biomanipulation: Round Lake, Minnesota, the first two years. Freshwater Biol. 14: 371–383.

SOKAL, R. R., AND F. J. ROHLF. 1969. Biometry. W. H. Freeman and Co., San Francisco, CA.

SOURNIA, A. 1978. The phytoplankton manual. United Nations Educational, Scientific and Cultural Organization, Paris, France.

SPENCER, C. N., AND D. L. KING. 1984. Role of fish in regulation of plant and animal communities in eutrophic ponds. Can. J. Fish. Aquat. Sci. 41: 1851–1855.

SWINGLE, H. S. 1950. Relationships and dynamics of balanced fish populations. Bull. No. 274. Agric. Exp. Stn., Alabama Poly. Inst.

WERNER, E. E., J. F. GILLAM, D. J. HALL, AND G. G. MITTELBACH. 1983. An experimental test of the effects of predation risk on habitat use in fish. Ecology 64: 1540–1548.

WERNER, E. E., AND D. J. HALL. 1976. Niche shifts in sunfishes: experimental evidence and significance. Science (Wash., DC) 191: 404–406.

WHITFORD, L. A., AND G. J. SCHUMACHER. 1973. A manual of fresh-water algae. Sparks Press, Raleigh, NC.

WINER, B. J. 1971. Statistical principles in experimental design. McGraw-Hill Book Company, New York, NY.

ZARET, T. M. 1980. Predation and freshwater communities. Yale University Press, New Haven, CT.

ZARET, T. M., AND R. T. PAINE. 1973. Species introduction in a tropical lake. Science (Wash., DC) 182: 449–455.

Seasonal Inorganic Carbon and Nitrogen Transport by Phytoplankton in an Arctic Lake[1]

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Euphotic zone profiles of dissolved inorganic carbon (DIC = CO_2 + HCO_3^- + CO_3^{2-}) and nitrogen (DIN = NO_3^- + NH_4^+) transport were taken from Toolik Lake, Alaska, at approximately 10-d intervals through 100-d growing seasons in 1980 and 1981. Rates of DIC transport ranged from <0.2 to 7.8 μmol·L^{-1}·d^{-1}, with the maximum always at 0–1 m. Nitrate and ammonium transport rates ranged from <0.1 to 3 and 0.4 to 8 nmol·L^{-1}·d^{-1}, with the vertical pattern variable. For the 1980 and 1981 investigative periods, DIC transport was 622 and 504 mmol·m^{-2} (7.5 and 6.0 g C·m^{-2}), making Toolik one of the most oligotrophic lakes on record. DIN transport for the respective years was 34 and 41 mmol·m^{-2}, giving molar C/N transport ratios of 18 and 12. For both years, NO_3^- was <20% of total DIN transport. Half-saturation constants for NO_3^- and NH_4^+ transport were similar, averaging ($\bar{X}$ ± SD) 0.11 ± 0.08 and 0.15 ± 0.13 μmol·L^{-1}. During the ice-free period, mean turnover times were also comparable at 6.3 ± 8.2 (NO_3^-) and 2.6 ± 1.2 d (NH_4^+), while relative preference indices for both nutrients were often near 1.0, indicating transport equitable with availability. The total data show a population well adapted to utilize consistently low ambient concentrations of NO_3^- and NH_4^+ (0.05–0.20 μmol·L^{-1}) in the ice-free season, but incapable of exploiting elevated (2–3 μmol·L^{-1}) under-ice levels of NO_3^-.

Les profils du transport dans la zone euphotique du carbone et de l'azote inorganiques dissous (CID = CO_2 + HCO_3^- + CO_3^{2-} et NID = NO_3^- + NH_4^+) du lac Toolik (Alaska) ont été déterminés à environ 10 jours d'intervalle tout au long des 100 jours des saisons de croissance de 1980 et 1981. La gamme des taux de transport du CID était de <0,2 à 7,8 μmol·L^{-1}·jour^{-1}, et la valeur maximale était toujours notée dans la couche de 0–1 m. Les gammes de transport du nitrate et de l'ammonium étaient de <0,1 à 3 et de 0,4 à 8 nmol·L^{-1}·jour^{-1}, et présentaient une allure verticale variable. Au cours des périodes d'étude de 1980 et 1981, le transport du CID était de 622 et 504 mmol·m^{-2} (7,5 et 6,0 g·m^{-2} de C), ce qui fait du lac Toolik l'un des lacs les plus oligotrophes connus. Les taux de transport du NID étaient respectivement de 34 et 41 mmol·m^{-2} pour ces années, ce qui correspond à des taux de transport molaires C/N de 18 et 12. Au cours des deux années, le transport du NO_3^- était inférieur à 20 % du transport total du NID. Les constantes de demi-saturation pour le transport du NO_3^- et du NH_4^+ étaient semblables et s'élevaient, en moyenne ($\bar{X}$ ± ET) à 0,11 ± 0,08 et 0,15 ± 0,13 μmol·L^{-1}. Les temps de renouvellement, au cours de la période libre de glace, étaient aussi semblables et s'élevaient à 6,3 ± 8,2 jours (NO_3^-) et à 2,6 ± 1,2 jours (NH_4^+). Les indices de préférence relatifs pour ces deux matières nutritives se situaient souvent aux environs de 1,0; ce qui indique un transport correspondant à la disponibilité. L'ensemble des données montre l'existence d'une population bien adaptée pour utiliser les faibles concentrations ambiantes en NO_3^- et NH_4^+ (0,05 – 0,20 μmol·L^{-1}) au cours de la saison libre de glace, mais qui est incapable de tirer profit des teneurs élevées en NO_3^- (2–3 μmol·L^{-1}) que l'on rencontre sous les glaces.

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This investigation tracks the seasonality of phytoplankton utilization of dissolved inorganic carbon (DIC = CO_2 + HCO_3^- + CO_3^{2-}) and dissolved inorganic nitrogen (DIN = NO_3^- + NH_4^+) in Toolik Lake, Alaska. Specifically, our goals were to examine the relationship between phytoplankton productivity and DIN uptake, extent of use of each DIN form relative to availability, and adaptation of indigenous populations to utilize efficiently the standing stock of nutrient. The present study represents one component of a program investigating DIN supply, phytoplankton productivity, and their interactions in this nitrogen-poor arctic lake. Previously, we reported short-term (diel) variations in primary biosynthesis and DIN uptake (Whalen and Alexander 1984a) and physical (light, temperature) influences on DIN utilization (Whalen and Alexander 1984b).

Earlier lacustrine studies with an experimental aim similar to ours have generally relied on seasonal analysis of a euphotic zone composite or a single, near-surface sample (e.g. Axler et al. 1982). Here, comprehensive depth profiles of many important variables often allowed for area-based data interpretation (i.e. per square metre of lake surface), which may yield more meaningful conclusions in an ecosystem context.

Toolik Lake is located at 68°38′N and 149°38′W on the northern flanks of the Brooks Range. The physical and chemical limnology have been discussed in detail by Whalen and Cornwell (1985). Briefly, the lake surface covers 1.5 km^2 and maximum and mean depths are 25 and 7 m. A single outlet and two major inlet streams flow from mid-May through

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mid-September. The ice-free period is brief (late June until late September), but thermal stratification usually develops for 5–6 wk in July and August. Maximum extent of the thermocline is 8–10 m with temperatures at the lake surface and bottom reaching 16 and 7°C. Bottom waters remain oxic year-round.

Materials and Methods

All water was pumped from a permanent deepwater station and prescreened through 202-μm Nitex mesh to exclude large zooplankton. Clear 1.3- or 2.4-L polystyrene containers were used in ^{15}N uptake experiments, while 0.165-L borosilicate glass bottles were employed in ^{14}C uptake measurements. Radiocarbon and nitrogen isotope additions were as $NaH^{14}CO_3$ and as 99 atom-% $Na^{15}NO_3$ or $^{15}NH_4Cl$. All $^{15}NO_3^-$ and $^{15}NH_4^+$ uptake determinations were made in duplicate for each depth (uptake profiles) or level of nutrient addition (kinetic experiments), while a single opaque and triplicate clear bottles were used to assess ^{14}C uptake at each depth.

A total of 20 vertical profiles of DIC and DIN uptake by Toolik phytoplankton were obtained during the 1980 and 1981 sampling seasons (mid-May through early September). Each sampling session was initiated at 06:00 local time by measuring the attenuation of photosynthetically active radiation (PAR) through the water column with a LiCor deck unit (LI 185) and flat plate underwater quantum sensor (LI 192S). Water from five or six depths to a point about 2 m beyond the estimated bottom of the euphotic zone (defined as the depth of 0.5% surface PAR penetration, following Fee 1980) was dispensed into appropriate containers and additions of 3.07 μmol $^{15}N \cdot L^{-1}$ or 315–575 kBq $^{14}C \cdot L^{-1}$ were made. Bottles were suspended at the depths of sample collection for 24 h beginning at about 08:00.

The kinetics of DIN uptake were assessed on six dates during each year. Samples drawn from the midepilimnion (3 m) received serial nutrient additions (eight concentrations per experiment, ranging from 0.1 to 2.0 μmol $^{15}N \cdot L^{-1}$ in 1980 and from 0.1 to 3.3 in 1981) and were incubated at 1 m from about 10:00 to 14:00.

In all experiments, water was reserved from each sample depth for additional biological and physicochemical analyses. Duplicate chlorophyll *a* (Chl *a*) (mean coefficient of variation, CV ± SD, at 1 m = 4 ± 4%; 20 data pairs) and particulate nitrogen (PN) (CV at 1 m = 7 ± 6%; 20 data pairs) determinations were made by fluorometric analysis of acidified and unacidified acetone extracts (Strickland and Parsons 1972) and persulfate oxidation (Solórzano and Sharp 1980), respectively. Single nitrate ($NO_3^- + NO_2^-$) and ammonium determinations were made by the Cu–Cd reduction and phenolhypochlorite methods (all samples stored frozen) following the AutoAnalyzer techniques of Whitledge et al. (1981). Our unpublished data from other Toolik experiments show that at typically encountered concentrations of NO_3^- (0.04–0.10 μmol $\cdot L^{-1}$) and NH_4^+ (0.05–0.20 μmol $\cdot L^{-1}$), CVs of 19 ± 15 and 15 ± 2% can be expected. Temperature measurements were made by immersing a hand-held thermometer in the pump outflow and total alkalinity was determined potentiometrically following Golterman et al. (1978).

Incubations were ended by filtration (<20 cm Hg) of the entire contents of each sample vessel onto uncombusted (^{14}C) or combusted (^{15}N; 6 h at 450°C) Gelman A/E glass fiber filters. Following a rinse with 25–50 mL of filtered lake water, filters were air-dried (^{14}C) or frozen and subsequently dried at 60°C (^{15}N). The ^{15}N content of filter-trapped particulate matter (range 0.1–11.1 atom-% excess) was measured in a Bendix model 17-210 mass spectrometer using a modified Dumas technique (Fiedler and Proksch 1975), while beta activity (^{14}C) was determined by liquid scintillation spectrometry (Beckman LS100C instrument; 5 mL of Aquasol-2 fluor).

Generally, we report uptake rates for DIC and DIN as ρ, the absolute transport rate, with units of nanomoles substrate utilized per volume per time. However, when data are best expressed in a biomass-independent manner, we give $\rho \cdot Chl^{-1}$, the chlorophyll-specific transport rate, with units of nanomoles substrate utilized per microgram Chl *a* per time.

Daily rates of ρ(C) were calculated as the difference between quench-corrected (channel ratio technique) light and dark bottle estimates times 1.06 (isotope correction; Vollenweider 1974) times a factor of 1.16 found necessary (Whalen and Alexander 1984a) to equate results of day-length experiments to the sum of consecutive short-term incubations over 24 h. The CV for 20 triplicate determinations of ρ(C) at 1 m was 5 ± 4%. Available ^{12}C was calculated from alkalinity, pH, and temperature measurements according to Golterman et al. (1978).

Directly determined rates of DIN transport in euphotic zone profiles (CVs for 20 data pairs at 1 m averaged 13 ± 7 and 13 ± 6% for NO_3^- and NH_4^+) are considered to be "measured-enhanced" (MacIsaac and Dugdale 1972) because our ^{15}N additions greatly exceeded ambient ^{14}N nutrient levels. The rate of nutrient transport can often be related to its extracellular concentration (S) via the following Michaelis–Menten relationship (MacIsaac and Dugdale 1972):

$$(1) \quad \rho = \rho_m \frac{S}{K_t + S}$$

where K_t (half-saturation constant) is the substrate concentration necessary to achieve half the maximum transport rate, ρ_m. Equation (1) was directly fitted (i.e. no linear transform) to kinetic experiment data by a least-squares technique (Cleland 1967) and K_t evaluated. The value of K_t obtained closest to the date of each DIN transport profile was used in conjunction with the measured-enhanced transport rate (ρ) and nutrient concentration at which it was made (S = ambient ^{14}N plus added ^{15}N) to estimate from equation (1) ρ_m for NO_3^- and NH_4^+ at each depth. The in situ day-rate value of ρ for NO_3^- was then computed by substituting in equation (1) ρ_m, the ambient NO_3^- concentration (S), and K_t, assuming that the latter remained constant with depth. Similar protocol was used to calculate daily NH_4^+ transport in situ, except ρ was multiplied by a factor of 1.4. This is in accordance with our previous study (Whalen and Alexander 1984a) assessing the relationship between estimates of daily NH_4^+ transport from 24-h exposures versus consecutive short-term incubations over an entire day.

Extinction coefficients (η) for PAR through the water column were calculated according to Vollenweider (1974) and the bottom of the euphotic zone (z_e) from the relationship $z_e = 5.3(\eta)^{-1}$. Values for biological and chemical variables at z_e were computed by linear interpolation between the most proximal data above and below z_e. Euphotic zone estimates of nutrients (Σ[N]) and Chl *a* (ΣChl), as well as day-rates of transport (Σρ), were made by summing the product of the value for each variable within a lake stratum times the volume of water in that stratum and dividing the sum by the lake surface area (square metres). Similarly, these resultant data were expanded over time to give seasonal estimates of transport per square metre of

TABLE 1. Kinetic parameters for NO_3^- and NH_4^+ transport, Toolik Lake phytoplankton. Values of the half-saturation constant K_t ($\mu mol \cdot L^{-1}$) and maximum transport rate ρ_m ($nmol \cdot L^{-1} \cdot h^{-1}$) calculated by direct, least-squares fit of Michaelis–Menten equation to transport–concentration data. Also given are the water temperature (°C), chlorophyll-specific maximum transport rate $\rho_m \cdot Chl^{-1}$ ($nmol\ N \cdot \mu g\ Chl^{-1} \cdot h^{-1}$), and $\rho_m \cdot Chl^{-1}$ equated to 10°C with a temperature coefficient (Q_{10}) of 2.3. *Data apparently do not conform to Michaelis–Menten kinetics.

		Kinetic parameters							
		NO_3^--N		NH_4^+-N		$\rho_m \cdot Chl^{-1}$		$\rho_m \cdot Chl^{-1}$ equated to 10°C	
Date	Temp.	K_t	ρ_m	K_t	ρ_m	NO_3^-	NH_4^+	NO_3^-	NH_4^+
1980									
20 June	4	*	*	0.05	4.4	—	2.7	—	4.8
6 July	13	0.25[a]	9.5	0.49[a]	17.1	4.0	7.3	3.3	6.1
16 July	15	0.12[a]	3.0	0.17[a]	5.7	2.7	5.2	1.9	3.7
7 Aug.	10	0.07[a]	3.3	0.15[a]	6.2	2.8	5.0	2.8	5.0
21 Aug.	9	0.10	2.1	*	*	1.5	—	1.7	—
4 Sept.	5	0.30	0.6	0.11	1.8	0.4	1.2	0.7	2.0
1981									
5 June	3	0.05	4.8	*	*	0.9	—	1.7	—
12 June	5	0.04	1.8	0.15	5.5	1.5	4.6	2.5	7.6
9 July	7	0.06	4.4	0.06	6.4	1.7	2.5	2.4	3.5
28 July	14	0.09	4.6	0.08	10.0	3.8	8.3	2.9	6.4
11 Aug.	12	0.10	3.3	0.09	7.8	3.0	7.1	2.7	6.3
16 Aug.	10	0.07	2.6	*	*	2.2	—	2.2	—

[a]Data from Table I in Whalen and Alexander (1984a).

lake surface ($\Sigma\Sigma\rho$).

Weighted turnover times (TT) and relative preference indices (RPI) for NO_3^- in the euphotic zone were calculated as

$$(2)\quad TT(NO_3^-) = \frac{\Sigma[NO_3^-]}{\Sigma\rho(NO_3^-)}$$

and

$$(3)\quad RPI(NO_3^-) = \frac{\Sigma\rho(NO_3^-)/\Sigma\rho(DIN)}{\Sigma[NO_3^-]/\Sigma[DIN]}$$

where all parameters are as previously defined. Turnover times and RPIs for NH_4^+ were computed analagously, where NH_4^+ replaces NO_3^- in equations (2) and (3).

Results

Kinetic Experiments for DIN Transport

In one kinetic experiment for NO_3^- and three for NH_4^+, transport was apparently non-Michaelian (Table 1), as ρ decreased slightly with increasing substrate (data not shown). In all other cases, however, saturation kinetics were observed. Resultant half-saturation constants for NH_4^+ transport ranged from 0.05 to 0.49 $\mu mol \cdot L^{-1}$ (Table 1). These were on the same order as ambient NH_4^+ levels, which varied from 0.12 to 0.32. Values of $K_t(NO_3^-)$ and ambient NO_3^- concentrations were also similar, showing ranges of 0.05–0.30 (Table 1) and 0.04–0.15 $\mu mol \cdot L^{-1}$. No seasonal pattern for $K_t(NO_3^-)$ or $K_t(NH_4^+)$ was found, although the second highest value of the former (0.25 $\mu mol \cdot L^{-1}$) was coincidental with the highest for the latter (0.49 $\mu mol \cdot L^{-1}$) on 6 July 1980. Overall mean ($\bar{X} \pm SD$) K_t values for NO_3^- (0.11 ± 0.08 $\mu mol \cdot L^{-1}$) and NH_4^+ (0.15 ± 0.13) were not significantly different (Student's t-test; df = 18, $P = 0.49$).

For the eight dates where matching data were available (Table 1), $\rho_m(NH_4^+)$ was significantly greater than $\rho_m(NO_3^-)$ (paired t-test; df = 7, $P < 0.01$). The total data for $\rho_m(NO_3^-)$ and $\rho_m(NH_4^+)$ ranged over factors of about 16 (0.6–9.5 $nmol \cdot L^{-1} \cdot h^{-1}$) and 10 (1.8–17.1), with variability in part attributable to temporal differences in the magnitude of the standing crop. Thus, biomass-independent date ($\rho_m \cdot Chl^{-1}$) showed a reduction in variability of 30–37% (Table 1). Significant correlations were found between water temperature and rates of maximum chlorophyll-specific transport for both NO_3^- (Spearman's rank correlation coefficient; $r_s = 0.86$, df = 9, $P < 0.01$) and NH_4^+ ($r_s = 0.80$; df = 7, $P < 0.02$), indicating a thermal influence on $\rho_m \cdot Chl^{-1}$. Elimination of this effect by equating $\rho_m \cdot Chl^{-1}$ to 10°C with a temperature coefficient (Q_{10}) of 2.3 (Whalen and Alexander 1984b) further diminished data variability as values ranged from 0.7 to 3.3 and 2.0 to 7.6 $nmol\ N \cdot \mu g\ Chl^{-1} \cdot h^{-1}$ for NO_3^- and NH_4^+ transport (Table 1), or over factors of about 5 and 4.

Seasonal Depth Profiles

The euphotic depth ranged from 1.8 to 9.3 m (Table 2). The lowest value for each year occurred on the first sampling date, before the snow pack on the ice had melted. A general increase in z_e was observed through the 1981 sampling season, but there was no pattern for 1980.

Euphotic Chl *a* concentrations ranged from 0.5 to 5.4 $\mu g \cdot L^{-1}$. Seasonally, highest concentrations were found in the sping, at 0–1 m beneath the ice bottom (Fig. 1A). Immediately following ice-out in late June of both study years, this near surface maximum was replaced by a homogeneously distributed Chl *a* concentration of about 2.5–3.0 $\mu g \cdot L^{-1}$. With the early July onset of thermal stratification in 1980, a metalimnetic Chl *a* maximum developed (Fig. 1B), with concentrations at depth sometimes three- to four-fold higher than at the surface. Sampling to the lake bottom on selected dates (data not shown) revealed that this subsurface maximum originated as a sharp peak at 5 m and progressed to a broad 4- to 6-m band extending

TABLE 2. Seasonal variations in some physical and area-based biological characteristics of Toolik Lake euphotic zone, 1980 and 1981. Included are euphotic depths (z_e, in metres), turnover times (TT, in days), relative preference indices (RPI), dissolved inorganic carbon transport rates ($\Sigma\rho$(C), in mmol·m^{-2}·d^{-1}), chlorophyll-specific rates of dissolved inorganic nitrogen transport ($\Sigma\rho$(DIN)/ΣChl, in nmol N·μg Chl^{-1}·d^{-1}), and molar ratios of dissolved inorganic carbon to nitrogen transport at ambient ($\Sigma\rho$(C)/$\Sigma\rho$(DIN)) and transport-saturating ($\Sigma\rho$(C)/$\Sigma\rho_m$(DIN)) levels of DIN.

		TT		RPI					
Date	z_e	NO_3^-	NH_4^+	NO_3^-	NH_4^+	$\Sigma\rho$(C)	$\Sigma\rho$(DIN)/ΣChl	$\Sigma\rho$(C)/$\Sigma\rho$(DIN)	$\Sigma\rho$(C)/$\Sigma\rho_m$(DIN)
1980									
22 May	1.8	36	2.0	0.16	3.0	2.02	78	13.6	9.7
29 May	5.9	93	3.8	0.24	6.1	4.91	55	21.8	16.8
7 June	5.7	85	3.6	0.21	4.9	3.81	33	17.5	12.6
24 June	6.1	10	2.3	0.36	1.6	12.51	31	35.9	23.1
1 July	7.7	2.7	1.7	0.80	1.0	5.31	44	10.9	23.3
18 July	7.5	6.6	2.0	0.32	1.0	3.26	81	7.2	3.1
24 July	7.2	4.5	2.5	0.63	1.2	4.57	52	15.6	6.4
5 Aug.	8.0	2.9	1.7	0.68	1.2	7.04	59	17.7	7.4
10 Aug.	6.4	4.2	2.7	0.74	1.2	6.47	54	20.7	10.5
19 Aug.	7.2	9.4	4.4	0.56	1.2	6.70	48	22.4	13.2
2 Sept.	7.4	35	5.8	0.21	1.4	6.05	24	40.6	22.2
1981									
3 June	3.4	24	1.5	0.43	6.8	5.50	58	21.2	21.2
10 June	5.3	62	4.9	0.36	4.6	4.59	71	13.7	10.0
6 July	6.3	2.3	2.0	0.92	1.0	10.40	35	23.7	14.4
14 July	8.0	1.8	1.8	1.00	1.0	6.90	50	12.1	7.6
23 July	7.1	2.3	1.9	0.83	1.0	5.04	133	7.0	4.6
30 July	8.0	3.7	2.8	0.81	1.0	5.02	84	9.0	6.1
8 Aug.	8.7	2.8	1.5	0.64	1.1	3.87	143	5.1	3.0
15 Aug.	9.3	4.9	3.6	0.81	1.0	3.83	63	10.3	6.4
25 Aug.	8.4	2.5	2.6	1.00	1.0	5.91	60	13.3	7.6

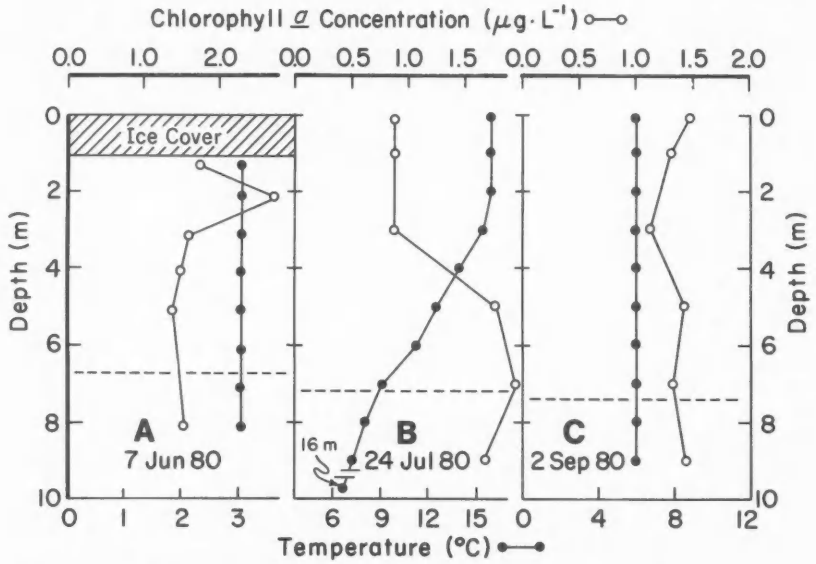

FIG. 1. Typical euphotic profiles of chlorophyll *a* and temperature in Toolik Lake (A) beneath ice cover in spring, (B) during midsummer, and (C) in the fall. Lower limit of euphotic zone indicated by horizontal broken line and ice cover to scale.

into the upper hypolimnion. By mid-August the mixed layer had reached 10 m, the thermocline had nearly eroded, and euphotic Chl *a* profiles were again orthograde and remained so for the balance of the sampling season (Fig. 1C). In 1981, thermal stratification occurred later and for an abbreviated time (late July to late August). A sharply defined thermocline never developed (maximum temperature difference between lake surface and bottom was 4.6°C) and a deep Chl *a* maximum was apparent only on 23 July, with euphotic distributions otherwise homogeneous during the ice-free season.

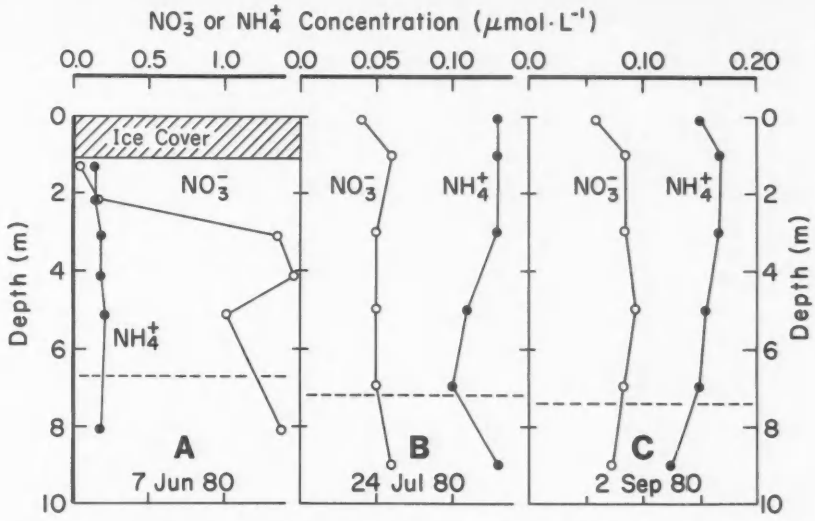

FIG. 2. Representative euphotic profiles of NO_3^- and NH_4^+ in Toolik Lake (A) beneath ice cover in spring, (B) during thermal stratification in midsummer, and (C) after fall overturn. Lower limit of euphotic zone indicated by horizontal broken line and ice cover to scale.

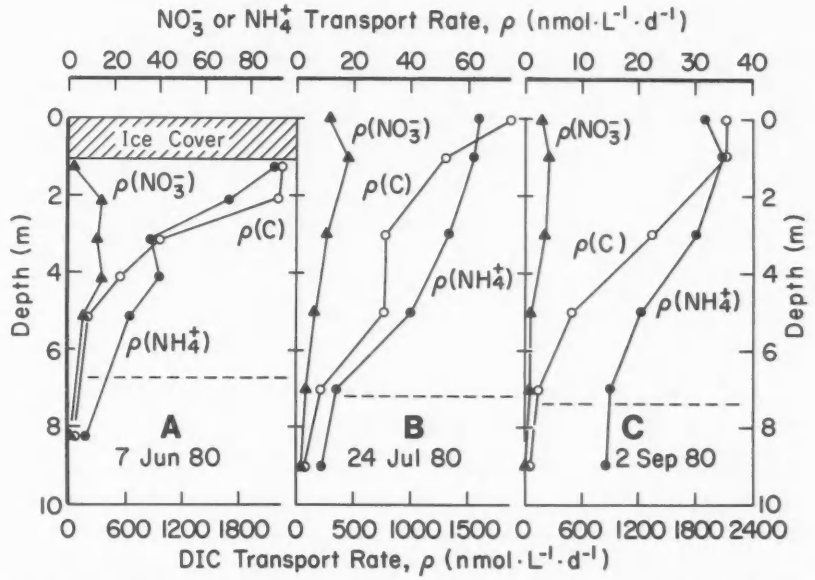

FIG. 3. Representative euphotic profiles for in situ transport of NO_3^-, NH_4^+, and dissolved inorganic carbon (DIC) in Toolik Lake (A) beneath ice cover in spring, (B) during thermal stratification in midsummer, and (C) after fall overturn. Lower limit of euphotic zone indicated by horizontal broken line and ice cover to scale.

Euphotic NO_3^- concentrations ranged from 0.04 to 2.9 $\mu mol \cdot L^{-1}$, while the range for NH_4^+ was considerably smaller (0.06–0.41). Elevated NO_3^- levels were consistently found from about 1–2 m below the ice to z_e (Fig. 2A). With ice-out, concentrations rapidly declined to an orthograde 0.05 $\mu mol \cdot L^{-1}$ and remained near that level both during thermal stratification (Fig. 2B) and autumnal circulation (Fig. 2C). Ammonium profiles were characterized by a lack of vertical structure during the entire investigation (Fig. 2A, 2B, 2C).

Transport rates for DIC were always highest at the lake surface or approximately equal at 0–1 m, but thereafter decreased to z_e (Fig. 3A, 3B, 3C), a pattern that persisted even when ρ(C) was normalized to Chl *a* (data not shown). Beneath the ice, $\rho(NO_3^-)$ was typically less than $\rho(NH_4^+)$ (Fig. 3A), despite higher ambient levels of NO_3^- (Fig. 2A). However, at a given depth during the open-water season, $\rho(NH_4^+)$ invariably exceeded $\rho(NO_3^-)$ by as much as a factor of 10 (Fig. 3B, 3C). Vertical profiles of $\rho(NO_3^-)$ and $\rho(NH_4^+)$ were variable,

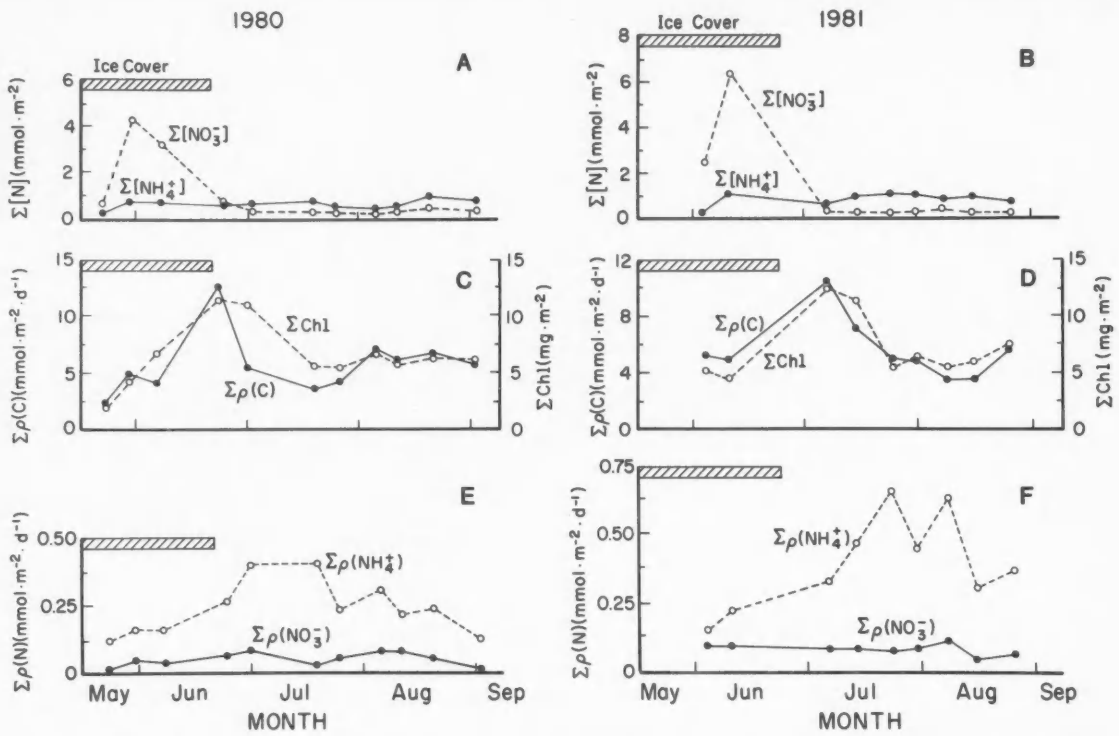

FIG. 4. Seasonal variations in area-based euphotic variables for Toolik Lake. (A, B) Ambient NO_3^- and NH_4^+ ($\Sigma[N]$); (C, D) phytoplankton chlorophyll *a* (ΣChl) and dissolved inorganic carbon transport ($\Sigma\rho(C)$); (E, F) dissolved inorganic nitrogen transport by phytoplankton ($\Sigma\rho(N)$).

reflecting their dependence on ambient nutrient levels and biomass as well as the decreased influence of PAR when compared with $\rho(C)$. As a rule, however, ρ(DIN) was greatest in the upper half of the euphotic zone. Despite this generalized decrease in ρ with increasing depth, $\rho(NH_4^+)$ at z_e was sometimes substantial, as much as 65% of the highest value at or near the lake surface (e.g. Fig. 3C).

Area-Based Data

On an areal basis, euphotic NO_3^- showed striking seasonal changes (Fig. 4A, 4B). Beneath ice cover, $\Sigma[NO_3^-]$ reached 4.4 and 6.4 mmol·m^{-2} in 1980 and 1981. The rapid increase in $\Sigma[NO_3^-]$ between the first two sampling dates of each year (Fig. 4A, 4B) resulted from a two- to three-fold increase in z_e (Table 2). With ice-out, $\Sigma[NO_3^-]$ rapidly decreased to about 0.3 mmol·m^{-2} and varied little to the end of the sampling season.

In contrast with $\Sigma[NO_3^-]$, $\Sigma[NH_4^+]$ did not show high under-ice values (Fig. 4A, 4B). In fact, the lowest $\Sigma[NH_4^+]$ for each year (approximately 0.2 mmol·m^{-2}) was observed on the first sampling date, with values increasing to about 0.7 (1980) and 1.0 (1981) on the second sampling date and remaining constant thereafter. Consequently, $\Sigma[NO_3^-]$ exceeded $\Sigma[NH_4^+]$ beneath the ice, with the situation reversed for the open-water period.

Euphotic zone Chl *a*, taken as an index of phytoplankton biomass, increased from the initiation of sampling to peaks of 11.6 and 12.5 mg·m^{-2} shortly after ice-out in 1980 and 1981 (Fig. 4C, 4D). A continuous decrease to about 6 mg·m^{-2} by late July followed in both years, with ΣChl remaining essentially constant thereafter except for a late August increase in 1981.

Rates of DIC transport per square metre of lake surface closely tracked ΣChl (Fig. 4C, 4D), with values ranging from 2.0 to 12.5 and 3.8 to 10.4 mmol·m^{-2}·d^{-1} for 1980 and 1981. Although the correlation coefficient between $\Sigma\rho(C)$ and ΣChl was highly significant, neither variable was significantly correlated with the euphotic temperature or z_e (Table 3).

Area-based transport rates for NO_3^- in the euphotic zone remained surprisingly low throughout both sample years (Fig. 4E, 4F), despite marked changes in $\Sigma[NO_3^-]$ (Fig. 4A, 4B). The total data varied from 0.01 to 0.12 mmol·m^{-2}·d^{-1}. In comparison, $\Sigma\rho(NH_4^+)$ was always higher than $\Sigma\rho(NO_3^-)$ by as much as an order of magnitude, with data ranging from 0.13 to 0.66 mmol·m^{-2}·d^{-1} (Fig. 4E, 4F). Highest values for both variables were observed during the ice-free period, but otherwise the data showed no seasonal pattern. Overall, increases in $\Sigma\rho(NH_4^+)$ were significantly correlated with increases in z_e and water temperature, but showed no relationship to biomass (ΣChl), $\Sigma\rho(NO_3^-)$, or $\Sigma\rho(C)$ (Table 3). On the other hand, $\Sigma\rho(NO_3^-)$ was not significantly correlated with any other euphotic variable tested (Table 3).

Turnover times for NH_4^+ showed little seasonal variation (Table 2). In contrast, $TT(NO_3^-)$ beneath ice cover (Table 2; data before 20 June) was considerably higher than open-water data (exception: 2 September 1980), resulting in a wide range of values. The difference between overall mean ($\bar{X} \pm$ SD) turnover times for NO_3^- (19.8 ± 28.4 d) and NH_4^+ (2.8 ± 1.2) was

TABLE 3. Spearman's rank correlation coefficients (r_s) for correlations between euphotic zone variables in Toolik Lake. Data from 1980 and 1981 were pooled (df = 18, all cases) and all biological variables were expressed on an areal basis (per square metre of lake surface). Values of $r_s > 0.45$ are statistically significant ($P < 0.05$).

	r_s					
	z_e	°C	ΣChl	Σρ(C)	$\Sigma\rho(NO_3^-)$	$\Sigma\rho(NH_4^+)$
Euphotic depth, z_e	1.00					
Temperature, °C	0.70	1.00				
Chlorophyll *a*, ΣChl	0.35	0.09	1.00			
Inorganic C transport rate, Σρ(C)	0.07	−0.10	0.65	1.00		
NO_3^- transport rate, $\Sigma\rho(NO_3^-)$	0.12	0.16	0.10	0.33	1.00	
NH_4^+ transport rate, $\Sigma\rho(NH_4^+)$	0.68	0.71	0.35	0.10	0.42	1.00

significant (Student's *t*-test; df = 19, $P < 0.02$). However, for the ice-free period, the difference between means for turnover of NO_3^- (6.3 ± 8.3 d) and NH_4^+ (2.6 ± 1.2) was not significant (Student's *t*-test; df = 14, $P = 0.11$).

The relative preference index of McCarthy et al. (1977) provides a measure of the use of a particular form of N relative to availability. A value of unity indicates transport equitable with availability, while lesser and higher values denote rejection and preferential utilization, respectively. RPIs for NO_3^- and NH_4^+ consistently showed a pronounced early season selection against the former and for the latter nutrient (Table 2). This trend was relaxed considerably for the ice-free period of 1980, while the open-water season of 1981 was characterized by balanced transport and availability for NH_4^+ and mild rejection or balanced transport and availability for NO_3^-.

Volume-weighted rates of chlorophyll-specific transport for DIN were nonuniform, and no seasonal trend existed for either year (Table 2). Overall, the data ranged from 24 to 143 nmol $N \cdot \mu g\ Chl^{-1} \cdot d^{-1}$, with highest values found in 1981.

Low ambient DIN levels led to high areal C/DIN transport ratios by moles (Table 2), the average ($\bar{X}$ ± SD) for the entire study being 17.0 ± 9.1. By comparison, the mean ratio at transport-saturating levels of DIN was 32% lower, 11.5 ± 6.7. Ratios for C/DIN transport at both ambient and saturating concentrations were in general lowest in mid-July, increasing at both ends of the sampling season.

Seasonal Summaries

Euphotic DIN transport totalled 34 and 41 $mmol \cdot m^{-2}$ during the 1980 and 1981 investigative periods, with NO_3^- comprising <20% of the transport for both years (Table 4). DIC transport was 622 and 504 $mmol \cdot m^{-2}$ (7.5 and 6.0 g $C \cdot m^{-2}$) for the respective sample years, giving molar ratios of 18.3 and 12.3 for area-based C/DIN transport. Substrate-saturated DIN transport was 81 and 66 $mmol \cdot m^{-2}$ for 1980 and 1981, indicating that DIN transport at ambient nutrient levels was only 42 and 62% of the theoretical maximum. Under saturating conditions, molar C/DIN transport ratios were similar for both years (7.6 and 7.7). Based on our unpublished early and late season data from 1979, the most extensive data from this study (1980) probably underestimate annual DIC and DIN transport by about 15%.

TABLE 4. Seasonal summaries of area-based transport ($mmol \cdot m^{-2}$) for dissolved inorganic nitrogen (DIN) and carbon at ambient ($\Sigma\Sigma\rho$) and transport-saturating ($\Sigma\Sigma\rho_m$) levels of DIN, Toolik Lake euphotic zone. Also included are molar C/DIN transport ratios at ambient ($\Sigma\Sigma\rho(C)/\Sigma\Sigma\rho(DIN)$) and transport-saturating ($\Sigma\Sigma\rho(C)/\Sigma\Sigma\rho_m(DIN)$) levels of DIN.

Variable	22 May − 2 Sept. 1980	3 June − 25 Aug. 1981
$\Sigma\Sigma\rho(NO_3^-)$	6	8
$\Sigma\Sigma\rho(NH_4^+)$	28	33
$\Sigma\Sigma\rho$(DIN)	34	41
$\Sigma\Sigma\rho$(C)	622	504
$\Sigma\Sigma\rho_m(NO_3^-)$	21	17
$\Sigma\Sigma\rho_m(NH_4^+)$	60	49
$\Sigma\Sigma\rho_m$(DIN)	81	66
$\Sigma\Sigma\rho(C)/\Sigma\Sigma\rho(DIN)$	18.3	12.3
$\Sigma\Sigma\rho(C)/\Sigma\Sigma\rho_m(DIN)$	7.7	7.6

Discussion

Chlorophyll *a*

A subsurface Chl *a* maximum has been characterized in a multitude of north temperate lakes by an increase in viable biomass at a low light level, in or below a pronounced thermocline (e.g. Fee 1976; Priscu and Goldman 1983; Moll et al. 1984). Our data also exhibit these features. First, the Toolik subsurface maximum was associated with the strong summer 1980 thermocline (Fig. 1B), but was noted only once in poorly stratified 1981, and was located at the depth of 0.6−3% surface PAR. Second, good qualitative agreement exists between changes in PN and Chl *a* (for entire data $r_s = 0.50$, df = 112, $P < 0.01$), indicating that pigment increases accompanied biomass increases. Third, we found no change in Chl *a* quality (ratio of fluorescence before and after acidification; data not shown) from the lake surface through the deep maximum, an observation that was taken by Kalff et al. (1972) as evidence for a viable deep population.

Maintenance of the deep biomass maximum in Toolik was primarily via accumulation at depth of epilimnetic cells, with in situ growth of secondary importance. The absence of a summer nutricline (Fig. 2B) precludes as a causative factor active depth regulation in a high nutrient environment. Moreover, the subsurface maximum showed Chl *a* concentrations generally no greater than the homogeneous 2.5−3.0 $\mu g \cdot L^{-1}$ characteristic of vernal overturn, and peak concentrations decreased with time.

DIC Transport

The consistent observation in Toolik of maximum volumetric (Fig. 3) and chlorophyll-specific DIC transport at the lake surface or 0−1 m, followed by a decline to z_e, differed from

the seasonal pattern reported by Kalff and Welch (1974) for Canadian arctic Char Lake. From February to April in Char, the ρ(C) maximum occurred just beneath ice cover, descended and followed a ≤50 kcal·m^{-2}·d^{-1} isoline to 25 m (approximately the lake bottom) by mid-June, and ascended with an increase in its associated light intensity to the lake surface in August, indicating physiological adaptation. The authors further indicated that the ρ(C) maximum resulted from high ρ(C)·Chl^{-1}, rather than a shift in biomass.

The dissimilarity between lakes may stem from differences in temperature and transparency. As defined here, z_e sometimes extended to 25 m in Char (our calculation from white light data in Schindler et al. 1974), but never exceeded 9.3 m in Toolik (Table 2), giving a relatively greater photon flux at each metre increment in Char. Toolik euphotic water rapidly warmed to 15°C following ice-out, while Char never exceeded 5°C (Schindler et al. 1974). Talling (1957) and Bindloss (1974) noted an increase in I_k (light intensity at onset of light-saturated photosynthesis) with temperature for freshwater phytoplankton, while Rigler (1978) hypothesized that Char's low temperature retards photosynthetic adaptation to summer arctic light levels. Thus, the relatively warm and less transparent water of Toolik may aid in maintaining a close coupling between the photosynthetic optimum and 0- to 1-m values of PAR.

The annual DIC transport rate of about 620 mmol·m^{-2} for Toolik was roughly 2 times the 340 reported by Kalff and Welch (1974) for Char. This may be a consequence of Toolik's warmer temperature, longer open-water season (about 1 mo in Char; Kalff and Welch 1974), and greater external nutrient loading rate. Annual total N and P loads for Toolik were 290 and 4.6 mmol·m^{-2} (Whalen and Cornwell 1985), while the respective values for Char from the combined data of Schindler et al. (1974) and de March (1975) were 23 and 0.7. Concurrent productivity and nutrient budget data are lacking for other pristine arctic lakes.

DIN Transport and Kinetics

Half-saturation constants for DIN transport in Toolik (Table 1) are at least as low as any recorded for lacustrine phytoplankton. Such low values and the lack of statistical significance between means for $K_t(NO_3^-)$ and $K_t(NH_4^+)$ indicate a strong affinity for both DIN forms in Toolik.

The strong positive correlation between temperature and $\rho_m \cdot Chl^{-1}$ and the marked reduction in variability when data were normalized to 10°C (Table 1) point to the importance of temperature as an environmental regulator of ρ_m. These data corroborate well kinetic studies in laboratory cultures which also showed an increase in ρ_m(DIN) with temperature (Cloern 1977; Raimbault 1984).

On both an annual (Table 4) and daily (Fig. 4C, 4D, 4E, 4F) basis, euphotic values for areal transport of DIC and DIN underestimate whole lake activity due to continued transport below z_e, especially for NH_4^+ (e.g. Fig. 3C). However, this error was minimized by the small lake volume in deep strata. Our unpublished data from six 6-h midday incubations at seven standard depths from the lake surface to bottom in 1979 indicated that on the average ($\bar{X} \pm$ SD) 4 ± 3 and 7 ± 2% of area-based NO_3^- and NH_4^+ transport occurred below 8 m (z_e averaged 7.6 m during the ice-free portion of the present study). Similar analysis for DIC transport showed even less error, 2 ± 2%.

Temporally constant euphotic levels of NH_4^+ throughout this study and similar data for NO_3^- during the ice-free period (Fig. 4A, 4B) indicate a dynamic balance between supply and loss terms. This was not the case, however, for NO_3^- in the spring. Whole water column profiles for NO_3^- showed a net loss of 5.4 mmol·m^{-2} during 7–24 June 1980 with flux to the phytoplankton accounting for only 1.0, despite transport rates at >1 m beneath the ice that were not substrate limited. The mass balance for NO_3^- during the same period (Whalen and Cornwell 1985) showed a net riverine efflux of only 0.3 mmol·m^{-2}, leaving 76% of the disappearance unexplained. Loss to the periphyton represents an additional, unquantified flux, especially if moating and increased circulation stimulated benthic productivity. We calculate this to be about 50% of total photosynthesis in Toolik, based on data from Yeakel (1977) and G. Kipphut (Institute of Marine Science, University of Alaska, unpubl.). The feasibility of periphyton acting as a major sink for elevated spring NO_3^- is supported by a previous study (Axler et al. 1984) which showed this to be the most important factor effecting loss of NO_3^- from water of an oligotrophic lake following epilimnetic enrichment with NH_4NO_3. High volumetric NO_3^- transport observed here in association with an elevated spring substrate level has been reported for other lakes (Takahashi and Saijo 1981; Berman et al. 1984), but the area-based chemical and transport data needed to quantitatively reconcile NO_3^- disappearance and phytoplankton activity were lacking.

Intrinsically, a higher $\rho_m(NO_3^-) \cdot Chl^{-1}$ was needed for the spring phytoplankton to utilize effectively elevated early season NO_3^- levels. However, they were no better adapted to exploit this resource than summer assemblages in a characteristically low NO_3^- environment (cf. Fig. 4A, 4B and Fig. 4E, 4F). Normalization of $\Sigma\rho_m(NO_3^-)/\Sigma Chl$ to 10°C (Q_{10} = 2.3; Whalen and Alexander 1984b) and comparison of means ($\bar{X} \pm$ SD) for the ice-covered (40 ± 14 nmol N·μg Chl^{-1}·d^{-1}) and ice-free (32 ± 13) periods revealed no significant differences (Student's t-test; df = 18, P = 0.22). This is also seen in the limited data (Table 1) where temperature-normalized $\rho_m(NO_3^-) \cdot Chl^{-1}$ from 7–12 June 1981 (lake ice-covered) falls within the range for the ice-free period.

This seasonal constancy of $\rho_m(NO_3^-) \cdot Chl^{-1}$ (Table 1) and $\Sigma\rho_m(NO_3^-)/\Sigma Chl$ when temperature normalized (i.e. inability to utilize elevated spring NO_3^-) may have resulted from inhibition of $\rho_m(NO_3^-)$ by NH_4^+. Here, volume-weighted NH_4^+ ($\Sigma[NH_4^+]/z_e$) was only 0.06–0.21 μmol·L^{-1}. However, for other freshwaters, addition of 0.36 μmol $NH_4^+ \cdot L^{-1}$ to the ambient level of 0.03 reduced $\rho_m(NO_3^-)$ by 60% of that in unenriched samples (Priscu and Priscu 1984), and $\rho_m(NO_3^-)/\rho_m(NH_4^+)$ decreased with increasing NH_4^+, even at concentrations <0.5 μmol·L^{-1} (Takahashi and Saijo 1981). The latter authors hypothesized that such inhibition was advantageous in prolonging the residence time of elevated sping NO_3^-, thereby affording an additional DIN source for the summer phytoplankton when NH_4^+ levels were reduced. This argument is clearly inappropriate for Toolik, considering the rapid rate of NO_3^- loss in the spring (Fig. 4A, 4B) to sinks other than the phytoplankton.

In contrast with the spring, summer NO_3^- transport rates were substrate limited. In N-poor water, the ability to utilize simultaneously very low levels of NO_3^- and NH_4^+ would confer obvious ecological advantage. This capability is characteristic of the summer phytoplankton in Toolik. The observed saturation kinetics for NO_3^- transport in 4-h experiments on most dates (Table 1) and linearity from 2 to 24 h of $\rho_m(NO_3^-)$ in time-courses (Whalen and Alexander 1984a) argue for a persis-

tent transport capacity as opposed to induction of transport by experimental manipulation, a situation reported by Murphy (1980) for long-term (>8 h) incubations following substantial $^{15}NO_3^-$ additions. Moreover, for the ice-free period, the general proximity of $RPI(NO_3^-)$ and $RPI(NH_4^+)$ to 1.0 (Table 2) and lack of significant difference between means for $TT(NO_3^-)$ and $TT(NH_4^+)$ indicate a high phytoplankton demand for both NO_3^- and NH_4^+ as well as a lack of discrimination between available forms of DIN. McCarthy (1981) suggested that RPIs for NO_3^- and NH_4^+ will approach unity as DIN levels begin to restrict algal growth, a situation possible in Toolik considering the persistently low summer DIN (Fig. 4A, 4B).

Comprehensive ratios for carbon to DIN transport (Table 4) are markedly higher than the ratio of 6.5 expected for healthy algal biomass (Vallentyne 1974). However, our experiments did not evaluate respiratory loss of fixed DIC or transport of dissolved organic N (DON), both of which would decrease $\Sigma\Sigma\rho(C)/\Sigma\Sigma\rho(N)$. The former source of error is probably less in cold, high-latitude waters than in temperate or tropical lakes with a more sharply defined photoperiod (approximately <10–40% of photoassimilated DIC; Peterson 1980), but the latter may be important here. Budgetary considerations for 1980 (Whalen and Cornwell 1985) revealed that Toolik was a sink for total N, retaining 18% of the annual allochthonous input. Of the retained N, 96% was as DON. Cumulative evidence (review by Paul 1983; Jackson and Williams 1985) shows the importance of DON (e.g. urea, amino acids) as an algal nutrient source, at least for marine oligotrophic waters. Clearly, transport ratios given here demonstrate that ambient DIN was insufficient to meet phytoplankton needs, and that in the absence of an alternate nutrient supply (i.e. DON), N deficiency is likely. Nonetheless, $\Sigma\Sigma\rho(C)/\Sigma\Sigma\rho_m(DIN)$ closely approximated the optimal ratio of 6.5 (Table 4), indicating a physiological capability of meeting N requirements with DIN alone.

In summary, data given here point to a highly unproductive pelagic system with the spring phytoplankton incapable of exploiting elevated NO_3^- levels, and a summer population stressed for N, but well adapted to utilizing effectively limit of detection concentrations of both NO_3^- and NH_4^+.

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References

AXLER, R. P., R. M. GERSBERG, AND C. R. GOLDMAN. 1982. Inorganic nitrogen assimilation in a subalpine lake. Limnol. Oceanogr. 27: 53–65.

AXLER, R., J. REUTER, J. PRISCU, S. LOEB, R. CARLTON, J. ZEHR, AND C. GOLDMAN. 1984. Transformations of nitrogen following epilimnetic N-fertilization in Castle Lake, CA. 2. Nitrate and ammonium depletion pathways. Verh. Int. Ver. Limnol. 22: 583.

BERMAN, T., B. F. SHERR, E. SHERR, D. WYNNE, AND J. J. MCCARTHY. 1984. The characteristics of ammonium and nitrate uptake by phytoplankton in Lake Kinneret. Limnol Oceanogr. 29: 287–297.

BINDLOSS, M. E. 1974. Primary production of phytoplankton in Loch Leven, Kinross. Proc. R. Soc. Edinburg (B) 74: 157–181.

CLELAND, W. 1967. The statistical analysis of enzyme data, p. 1–32. *In* F. F. Nord [ed.] Advances in enzymology. Vol. 29. Interscience, New York, NY.

CLOERN, J. E. 1977. Effects of light intensity and temperature on *Cryptomonas ovata* (Cryptophyceae) growth and nutrient uptake rates. J. Phycol. 389–395.

DE MARCH, L. 1975. Nutrient budgets for a high arctic lake. Verh. Int. Ver. Limnol. 19: 496–503.

FEE, E. J. 1976. The vertical and seasonal distribution of chlorophyll in lakes of the Experimental Lakes Area, northwestern Ontario: implications for primary production estimates. Limnol. Oceanogr. 21: 767–783.

1980. Important factors for estimating annual phytoplankton production in the Experimental Lakes Area. Can. J. Fish. Aquat. Sci. 37: 513–522.

FIEDLER, R., AND G. PROKSCH. 1975. The determination of nitrogen-15 by emission and mass spectrometry in biochemical analysis: a review. Anal. Chim. Acta. 78: 1–62.

GOLTERMAN, H. L., R. S. CLYMO, AND M. A. M. OHNSTAD. 1978. Methods for physical and chemical analysis of fresh waters. International Biological Programme Handbook 8. 2nd ed. Blackwell Scientific Publications, Oxford. 213 p.

JACKSON, G. A., AND P. M. WILLIAMS. 1985. Importance of dissolved organic nitrogen and phosphorus to biological nutrient cycling. Deep-Sea Res. 32: 223–235.

KALFF, J., AND H. E. WELCH. 1974. Phytoplankton production in Char Lake, a natural polar lake, and in Meretta Lake, a polluted polar lake, Cornwallis Island, Northwest Territories. J. Fish. Res. Board Can. 31: 621–636.

KALFF, J., H. E. WELCH, AND S. K. HOLMGREN. 1972. Pigment cycles in two high-arctic Canadian lakes. Verh. Int. Ver. Limnol. 18: 250–256.

MACISAAC, J. J., AND R. C. DUGDALE. 1972. Interactions of light and inorganic nitrogen in controlling nitrogen uptake in the sea. Deep-Sea Res. 19: 209–232.

MCCARTHY, J. J. 1981. The kinetics of nutrient utilization, p. 211–233. *In* T. Platt [ed.] Physiological bases of phytoplankton ecology. Can. Bull. Fish. Aquat. Sci. 210: 346 p.

MCCARTHY, J. J., W. R. TAYLOR, AND J. L. TAFT. 1977. Nitrogenous nutrition of the phytoplankton in Chesapeake Bay. I. Nutrient availability and phytoplankton preferences. Limnol. Oceanogr. 22: 996–1011.

MOLL, R. A., M. Z. BRAHCE, AND T. P. PETERSON. 1984. Phytoplankton dynamics within the subsurface chlorophyll maximum in Lake Michigan. J. Plankton Res. 6: 751–766.

MURPHY, T. P. 1980. Ammonia and nitrate uptake in the Lower Great Lakes. Can. J. Fish. Aquat. Sci. 37: 1365–1372.

PAUL, J. H. 1983. Uptake of organic nitrogen, p. 275–308. *In* E. J. Carpenter and D. G. Capone [ed.] Nitrogen in the marine environment. Academic Press, New York, NY.

PETERSON, B. J. 1980. Aquatic primary productivity and the ^{14}C-CO_2 method: a history of the productivity problem. Annu. Rev. Ecol. Syst. 11: 359–385.

PRISCU, J. C., AND C. R. GOLDMAN. 1983. Seasonal dynamics of the deep-chlorophyll maximum in Castle Lake, California. Can. J. Fish. Aquat. Sci. 40: 208–214.

PRISCU, J. C., AND L. R. PRISCU. 1984. Inorganic nitrogen uptake in oligotrophic Lake Taupo, New Zealand. Can. J. Fish. Aquat. Sci. 41: 1436–1445.

RAIMBAULT, P. 1984. Influence of temperature on the transient response in nitrate uptake and reduction by four marine diatoms. J. Exp. Mar. Biol. Ecol. 84: 37–53.

RIGLER, F. H. 1978. Limnology in the high arctic: a case study of Char Lake. Verh. Int. Ver. Limnol. 20: 127–140.

SCHINDLER, D. W., H. E. WELCH, J. KALFF, G. J. BRUNSKILL, AND N. KRITSCH. 1974. Physical and chemical limnology of Char Lake, Cornwallis Island (75°N lat.). J. Fish. Res. Board Can. 31: 585–607.

SOLÓRZANO, L., AND J. H. SHARP. 1980. Determination of total dissolved nitrogen in natural waters. Limnol. Oceanogr. 25: 751–754.

STRICKLAND, J. D. H., AND T. R. PARSONS. 1972. A practical handbook of seawater analysis. 2nd ed. Bull. Fish. Res. Board Can. 167: 310 p.

TAKAHASHI, M., AND Y. SAIJO. 1981. Nitrogen metabolism in Lake Kizaki, Japan. I. Ammonium and nitrate uptake by phytoplankton. Arch. Hydrobiol. 91: 393–407.

TALLING, J. F. 1957. Photosynthetic characteristics of some freshwater phytoplankton diatoms in relation to underwater radiation. New Phytol. 56: 29–50.

VALLENTYNE, J. R. 1974. The algal bowl-lakes and man. Misc. Spec. Publ. 22, Dep. Environ., Fish. Mar. Serv., Ottawa, Ont. 185 p.

VOLLENWEIDER, R. A. 1974. A manual on methods for measuring primary productivity in aquatic environments. International Biological Programme Handbook 12. 2nd ed. Blackwell Scientific Publications, Oxford. 255 p.

WHALEN, S. C., AND V. ALEXANDER. 1984a. Diel variations in inorganic carbon and nitrogen uptake by phytoplankton in an arctic lake. J. Plankton Res. 6: 571–590.

1984b. Influence of temperature and light on rates of inorganic nitrogen transport by algae in an arctic lake. Can. J. Fish. Aquat. Sci. 41: 1310–1318.

WHALEN, S. C., AND J. C. CORNWELL. 1985. Nitrogen, phosphorus and organic carbon cycling in an arctic lake. Can. J. Fish. Aquat. Sci. 42: 797–808.

WHITLEDGE, T. E., S. C. MALLOY, C. J. PATTON, AND C. D. WIRICK. 1981. Automated nutrient analyses in seawater. Dep. Energy, Brookhaven National Lab. Assoc. Univ., Upton, NY. 216 p.

YEAKEL, J. D. 1977. Production and control of epilithic periphyton in an arctic lake. M.S. thesis, University of Cincinnatti, Cincinnatti, OH. 53 p.

Dynamics of Discovery and Exploitation: The Case of the Scotian Shelf Groundfish Fisheries

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The bases and shortcomings of the current models used in fisheries management are briefly examined. An alternative set of models in part based on the Volterra–Lotka equations are developed which incorporate recent advances in our understanding of the evolution of complex systems. Simulations based on a dynamic model of a Nova Scotia fishery reveal that human responses amplify rapid random fluctuations in recruitment and excite strong Volterra–Lotka type oscillations in a system that would normally repose in a stable stationary state. A dynamic, multispecies, multifleet spatial model calibrated to the Nova Scotian groundfish fisheries is presented and used to explore the concepts of "discovery" and "exploitation." Two types of fishermen are identified, "stochasts" and "cartesians," characterized respectively as hunters, or high risk takers, and followers, or low risk takers. Significant results include the importance of calibration in providing models of relevance to the real world; the "out of phase" relationship between abundance and the ease with which fishermen locate a highly sought species and its converse; the importance of information exchange in defining the attractivity of a particular fishing zone to different fleets and the ability of the model to take into account coded information, misinformation, spying and lying; and the fact that models based on global principles, such as "optimal efficiency" or "maximum profit," are clearly of dubious relevance to the real world.

Les auteurs font un bref examen des bases et des limitations des modèles actuellement utilisés en gestion des pêches. Ils présentent une autre série de modèles reposant en partie sur les équations de Volterra–Lotka qui tiennent compte des progrès récemment accomplis dans le domaine de l'évolution des systèmes complexes. Des simulations par modèle dynamique des pêches de la Nouvelle-Écosse montrent que les réponses humaines amplifient les fluctuations aléatoires rapides du recrutement et causent l'importantes oscillations de type Volterra–Lotka dans un système qui devrait normalement être dans un état stationnaire stable. Les auteurs présentent un modèle spatial dynamique à espèces et flottilles multiples étalonné en fonction des pêches du poisson de fond de la Nouvelle-Écosse et l'appliquent au concept de la « découverte » et de « l'exploitation ». On précise deux types de pêcheurs : les « stochastiques » et les « cartésiens » dont les caractéristiques respectives sont d'être des chasseurs, qui prennent des risques importants, et des adeptes, qui prennent peu de risques. On compte, parmi les résultats significatifs obtenus : 1) l'importance de l'étalonnage pour l'obtention de modèles pertinents aux conditions réelles, 2) le « décalage » de la relation entre l'abondance et la facilité avec laquelle les pêcheurs localisent les espèces très recherchées, ou l'inverse, 3) l'importance de l'échange d'information pour la définition de l'attrait d'une zone de pêche particulière pour les diverses flottilles et la capacité du modèle à tenir compte de l'information codée, de la mésinformation, de « l'espionnage » et des mensonges, et 4) le fait que les modèles basés sur des principes généraux, comme « l'efficacité optimale » ou le « profit maximal » apparaissent comme très nettement contestables quant à leur pertinence en conditions réelles.

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Fishing is one of the few remaining examples in the world today of ancestral hunting activities in humans. A key element of hunting is that it contains both "discovery" and "exploitation," rather than simply the latter which characterizes agriculture.

As we shall try to make clear below, fishing represents a fascinating "case study" of the much more general and wider issues of adaptiveness, creativity, and learning. This is interesting not only for itself and the role that new methods can play in managing such a vital industry, but also because of the general principles it raises. Within a problem having fairly clear boundaries, all the great questions of our relationship to nature, the problem of managing a complex system, and of finding a balance between yield and risk, are posed, and hopefully from this type of work, a new understanding will emerge both in the particular and general cases.

Commercial fisheries are part of the complex marine ecosystem involving ocean climate, hydrography, biological oceanography, and fish ecology, and also the human system including the behaviour and knowledge of fishermen, the requirements of

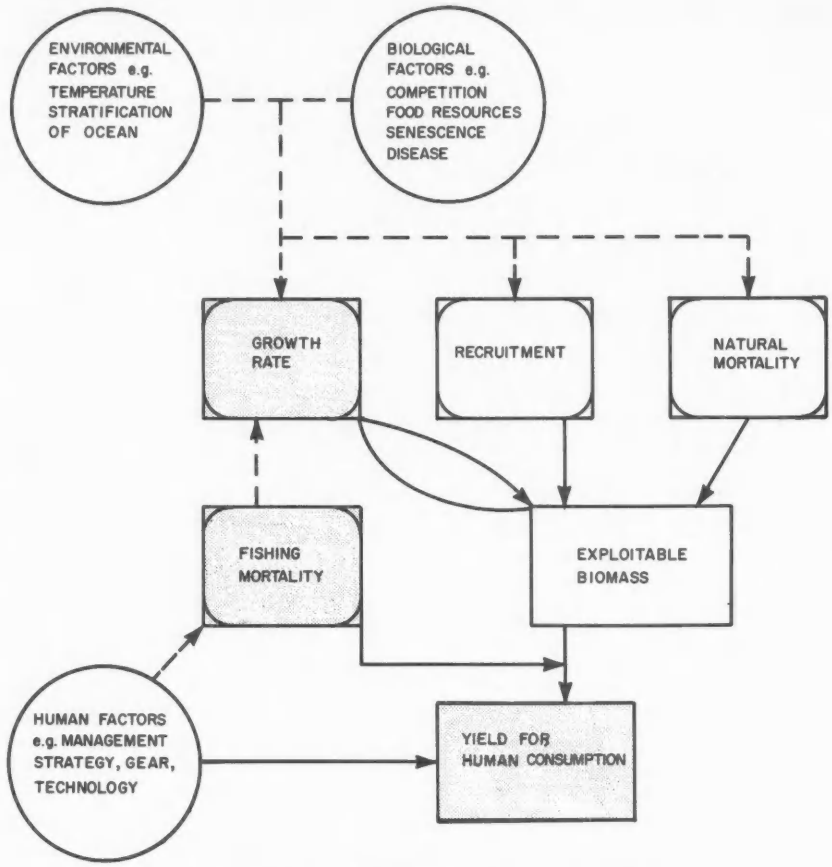

FIG. 1. Schematic diagram identifying areas of interest in fisheries.

the processing industry and markets for fish products, government policy, regulation, and political issues (Fig. 1) (McGlade and Allen 1985). Thus, fisheries science is not a discipline in itself, but rather the application of most of the basic sciences to the marine milieu and living resources of the seas. For example, the marine ecosystem, largely hidden from the human eye, is complex with respect to its species composition, as well as to the processes occurring within it. Thus, although we are really only interested in two of the apex predators, fish and man, we should be aware of the background against which their interaction is set, as shown in Fig. 1.

The interface of industry and fishermen with fisheries resources is multifaceted, and usually predicated by a knowledge of the resource distribution, demand, and availability (Kirby 1982; Pearse 1982). Fisheries will cause changes in the abundance of fish, such that the target species as well as those caught incidentally are likely to reflect trends in the market place as well as environmental and biological dynamics. If we add the consequences of technological changes, overcrowding in the littoral zones, and the impact of foreign fleets, it is evident that the "laissez-faire" attitude towards resource utilization that arose through the 1950's as a result of the persuasiveness of the scientific arguments is no longer a tenable stand for any level of government to take (Caddy 1983). To intervene in or monitor successfully such a complex system, and to formulate appropriate management schemes, it is important to identify the processes and causalities which serve to interrelate fish and their abundance, fishermen, fishery scientists, and managers, all of whom play an important role in the final yield of fish for human consumption. Yet it would be true to say that the multiplier effects such as employment in ancilliary activities, fishermen's employment, and their ability to move, plus the implications of the coexistence of inshore and offshore fleet components which should be integrated with information about the biological resource, are usually not dealt with explicitly in current management schemes.

Let us now turn to the recent advances that have been made in our understanding of the evolution of complex systems, as a result of the concepts underlying "dissipative structures." These have been discussed in detail elsewhere (Nicolis and Prigogine 1977; Prigogine and Allen 1982), and the main points which emerge are as follows.

(i) The evolution of such systems can be represented by an "evolutionary tree" of possible structures and organizations.

(ii) Any particular system will follow a trajectory through the tree which involves both the deterministic dynamics of "average" behaviours, and the effect of small chance phenomena at instabilities which can be amplified by the system and give rise to major changes. The tree itself can be profoundly modified by the presence of environmental distur-

bances, giving rise to fluctuating parameters.

(iii) The branches differ from each other qualitatively, having distinct traits and spanning different dimensions. In the case of a marine ecosystem, this could mean being populated by different species, in a set of alternative ecosystems.

In this paper, we consider a particular case study, that of fishery management and the groundfish fisheries off Nova Scotia, and discuss the existing types of model in use today.

Simple Fishing Models

The mathematical basis for the management of fish populations is rooted in the equations of population dynamics and mathematical ecology. There are two basic situations which are represented most often by the logistic equation, describing the growth of a single species in a limited environment, and the Volterra–Lotka equation describing the dynamics generated by a predator–prey interaction. All the rest are just concatenations of these, although additional refinements such as considerations of handling time and predator saturation can introduce important changes in the behaviour of the system (Jones and Walters 1976; Mangel 1982; Mangel and Beder 1985). Fishery management models in use today are only based on the logistic equation, although several complicating factors have been added such as population age structure and individual growth functions. We first examine these methods and their basis so that we may better appreciate their importance for the management of such systems.

Logistic Equation

This describes the growth of a single species in a limited environment. It can be made more complicated, taking into account the competition between different species which share the same resources, but its most simple and basic form is

$$(1)\quad \frac{dx}{dt} = bx\left(1 - \frac{x}{N}\right) - mx - Fx.$$

The first term on the right represents a density dependent "birth" term where the maximum niche size, N, sets a saturation level, mx corresponds to natural mortality, and the term Fx refers to the effect of fishing on the population. The fishing mortality, F, is related in standard theory to the catchability, q, of the fish and the fishing effort, E, exerted.

The term Fx is the yield, Y, of the system and provided that we assume equilibrium, it is easy to calculate yield as a function of F. The stationary solution of (1) is

$$x_s = N\left(1 - \frac{m + F}{b}\right)$$

and hence yield at equilibrium will be

$$(2)\quad Y = Fx_s = N\left(1 - \frac{m}{b}\right)F - \frac{N}{b}F^2.$$

This is a parabola, with a maximum value at $F = (b-m)/2$ the infamous F_{max}, "the maximum sustainable yield" which dominated the reflections of fishery managers prior to the last decade. Despite its extreme theoretical simplicity, attempts to guide fisheries to this maximum sustainable yield have proved extremely difficult. It seems that in a real system, levels of exploitation that are sustainable over a long period can only be found by trial and error, and in many fisheries this comes down to not having a management policy. Because of the rather mixed success of F_{max}, it was thought better to aim for a somewhat lower level of exploitation to reduce the risks of collapse in the system. In this way, $F_{0.1}$ was envisaged and defined as that level of fishing mortality giving rise to a slope on the yield-per-recruit/F curve of 1/10 that of the slope for a virgin fishery. In the simple logistic equation this turns out to be at $0.9F_{max}$, which is very close to a level of maximum exploitation, offering only a *narrow* safety margin.

We now consider the other pillar of mathematical ecology, which could have served as the basis for fishery management, but in fact did not.

Volterra–Lotka Equation

The important difference here is that the equations describe the interactions between species at two different levels in the system, a predator and its prey. The equations are

$$\frac{dx}{dt} = bx\left(1 - \frac{x}{N}\right) - sxy$$

$$\frac{dy}{dt} = sxy - my.$$

In the original work, N was assumed to be infinite, and the system gave rise to undamped cyclic oscillations of x and y around a neutrally stable stationary state, $x_s = m/s$: $y_s = b/s$. It was proposed as a basis to explain many of the oscillatory phenomena observed in natural populations, and it is interesting to note that Volterra's original work was performed in connection with the periodicities he had noticed in the populations of fish species in the Adriatic where he liked to go fishing. However, the neutrally stable (i.e. not stable) trajectories of this simple system with N infinite have been judged unsatisfactory as an explanatory model of observed behaviour, and many authors have insisted on the need to use a finite value of N. When this is done, the equations give rise to damped oscillations tending towards a stable stationary state, $x_s = m/s$ and $y_s = b(1 - m/Ns)/s$ (Fig. 2). Thus, they no longer offer an explanation of the oscillatory phenomena of natural populations. However, the addition of factors which take into account the effects given above, viz. handling time and predator saturation, can give rise to deterministic oscillatory solutions.

Historically, these equations did not form the basis of fisheries management. Instead the "logistic" approach was preferred. This reveals a basic reluctance of managers to treat "fishermen" as an active, responsive part of the whole system. The philosophy underlying the use of the logistic model is one in which the whole behaviour of the fishermen is subsumed and reduced to an "applied fishing mortality." Furthermore, by basing the calculation on an equilibrium hypothesis, this fishing mortality is supposed to remain constant at least for a time sufficient for the system to come to equilibrium. The whole question of the possible responses of the fishing industry to changing circumstances and profitabilities has been neglected, and it has been assumed that parameters such as b, m, and N can be represented simply by their average values, giving a deterministic relation between yield and fishing mortality. In addition, these models are nonspatial and refer to a population of a single species of fish.

It is not surprising that success in managing fisheries has been rather mixed.

Several developments have taken place in the past to construct better models on which to base management decisions. As early as 1957, Beverton and Holt developed the "Dynamic

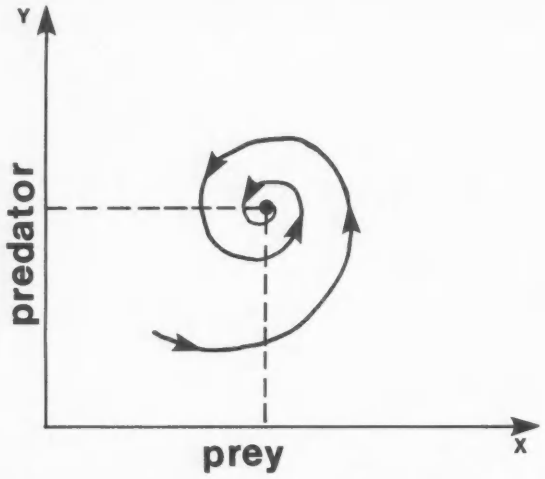

FIG. 2. Damped oscillations which characterize the approach to the stable, stationary state $x_s = m/s$ and $y_s = b(1 - m/Ns)/s$, which is the solution of the Volterra–Lotka equations with a limited carrying capacity for prey X and predator Y.

Pool Model," which was ostensibly a truly dynamic approach. Unfortunately, it came to fisheries scientists who were used to dealing with equilibrium, and thus some of the fundamental concepts became lost in static thinking. An important example is the yield per recruit (Y/R) calculation, which implicitly assumes that either constant fishing mortality or constant age structure holds. Considerable effort has been devoted to determining the "best" management strategies on the bases of the relationship between F and Y/R. The usual procedure is to compute the level of F that corresponds to some specified value of Y/R. As it may take 10 yr for a cohort to pass through a fishery, the calculation is invalid unless each age group suffers the same level of fishing mortality. The alternative of calculating an "instantaneous" Y/R based on the actual age pyramid is little better because it depends on the age structure remaining fixed throughout the life of each cohort. Beverton and Holt's objectives of moving towards a dynamic framework have therefore been frustrated, with equilibrium calculations prevailing in their stead.

Such methods have also been attacked in a series of papers by May and Beddington (Beddington 1979; Beddington and May 1977; May et al. 1979). They examined the effects of fluctuations in the value of parameters such as b, m, and N of the logistic equation. They showed that as exploitation increased the system moved towards instability and risked collapse. In a similar vein, work by Doubleday (1976), Nisbet and Gurney (1982), and Sissenwine (1984) showed the importance of fluctuations in natural systems. The idea that fluctuations around the average values of parameters could have an important impact on the sustainable catch had *not* been taken into account by managers aiming at high economic returns from "maximum sustainable exploitation rates." These were important results and have led to a further reduction in the confidence of management in the methods available to them, but have not resulted in any significant replacement by valid alternatives. Thus, it is pertinent to use the work of Hortsthemke and Lefever (1984) to show the effects of fluctuating parameters on

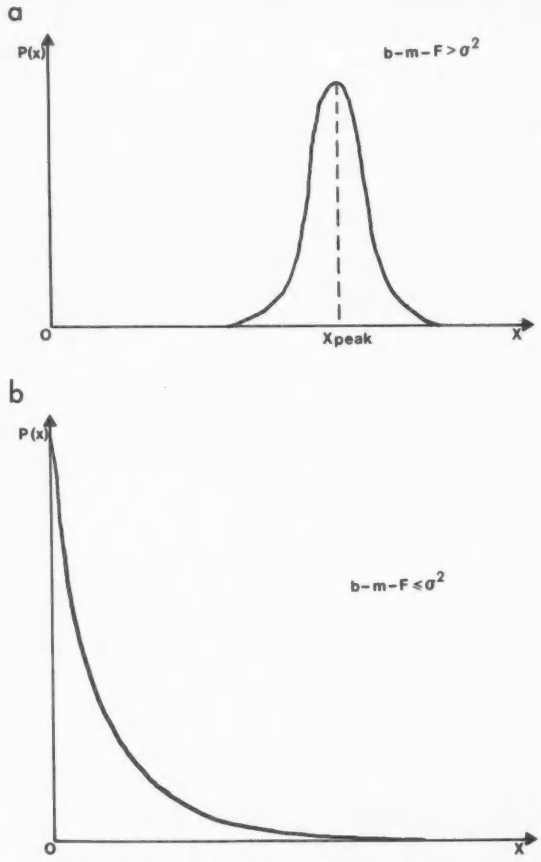

FIG. 3. Probability distribution curves of fish abundance (x), under a constant fishing mortality rate (F), where (a) $(\overline{b - m - F}) > \sigma^2$ and the $x_{\text{peak}} = N\left(1 - \dfrac{m + F + \sigma^2}{b}\right)$ and (b) $(\overline{b - m - F}) \leq \sigma^2$.

the logistic fishing model described earlier. As we shall see, it must fundamentally modify the very basis on which fishery models currently repose — the logistic description.

Logistic Fishing Model with Fluctuations

In the manner of Horsthemke and Lefever, we write the logistic equation taking into account the fact that in reality, at the very least, the birth rate b of a fish population such as haddock (*Melanogrammus aeglefinus*) fluctuates strongly around its average value:

$$(3)\quad dx = \left((\overline{b - m - F})x - \frac{b}{N}x^2\right)dt + \sigma^2 x dW_t.$$

The first terms gives the usual determinstic evolution, but the second term is a Wiener process which allows for the effects of fluctuations in b to be taken into account. The solution of this equation can be written

$$(4)\quad P_s(x) = \Omega e^{\frac{-bx}{N\sigma^2}} x^2 \left[\frac{(\overline{b - m - F})}{\sigma^2} - 1\right]$$

showing that the stationary probability distribution of x has a

form which is critically dependent on the sign of the term $[(b - m - F)/\sigma^2] - 1$. Thus, if $(b - m - F)$ is greater than σ^2, we have a distribution of the type shown in Fig. (3a). This corresponds to the previous deterministic situation, except that the x_{peak}, the most probable value, is at

$$x_{peak} = N\left(1 - \frac{m + F + \sigma^2}{b}\right)$$

which means it is displaced towards zero by the variance of the noise σ^2 in b. Although the fluctuations are both up and down, around the same average as before, the net effect is a decrease in the observed value of x. If fishing effort is increased so that $(b - m - F) < \sigma^2$, then the distribution $P_s(x)$ has $x = 0$ as the most probable value and an exponential type of tail of probability for finite values of x (Fig. 3b). In this situation there are most often no fish, but sometimes there are "bursts" of population which are fished rapidly out of existence. When fishing at F_{max}, it only requires $(b - m)/2 < \sigma^2$ for the transition to occur from a distribution of the first type to that of the second. The parameters and fluctuations for most groundfish (cod, haddock, pollock, etc.) certainly seem to fulfill this condition. Even when we fish at the "safer" limit of $F_{0.1}$, it turns out to provoke the same transition if $0.9(b - m)/2 < \sigma^2$ (McGlade and Allen 1985).

The basic description of a fishery thus requires modification because as F is changed and a collapse in x begins, then eventually fishing effort will also collapse as other activities, zones, or species become more attractive targets for fishermen. This switch may allow the rebuilding of the fish stocks, x, and later a return of fishing effort. What we really need to know is how fast fishing effort drops with decling returns on effort. How fast can fish stocks rebuild themselves? How fast does information about the size of a stock lead to an increase in fishing effort, an increase in information, and a repeat of the cycle? What we have just described is the basic logic underlying the Volterra–Lotka equation. Fundamentally we are arguing that fishery models should be based on *these concepts* rather than on the logistic equation, because, instead of viewing fishermen as purely passive elements, the Volterra–Lotka equation explicitly brings them and their reactions into the system to be modelled. To do this, and to show why in fact such a change was not immediately obvious, we turn to our case study, the groundfish fisheries of Nova Scotia.

Fishing for Groundfish off Nova Scotia

The main species of groundfish caught in this area are cod (*Gadus morhua*), haddock, and pollock (*Pollachius virens*). Each of these represents a "fishery," with management conducted according to spatial zones designed to coincide to a large extent with fish stocks. The data we consider are from NAFO (North Atlantic Fisheries Organization) Division 4*X*, over the period 1965–81.

In the previous sections we suggested that fisheries management must move away from simply considering fish populations and turn to models which include the behaviour of fishermen as an intrinsic part of their structure.

For example, a drop in yield may reflect the effects of several possible phenomena such as a decline in fish abundance, a decrease in fishing effort for reasons concerning profitability external to the fishery, or a reduction in the fisherman's knowledge about the location of fish aggregates. A Volterra–Lotka equation would only fit the first of these explanations, since it supposes cycles of fish abundance and effort, based on an endogenous logic, where external attractions are not supposed to influence the actors. Fishing effort and catch per unit effort are supposed to be mutually related and to give rise to cycles with lag between catch per unit effort and effort. To the really important question — are cyclic catastrophes in fisheries caused by natural events in the ecosystem outside of our control, or are they man-made — a pure Volterra–Lotka equation would suppose the latter. The real answer may be considerably more subtle.

Cod and pollock in the Division 4*X* show no Volterra–Lotka logic at all (Fig. 4a, 4b). Effort expended to catch fish is simply not related to the return on that effort. In contrast, haddock does exhibit something resembling a "cycle" (Fig. 4c). Can we explain these results and fit them into a coherent scheme? An answer appears as soon as one considers the question of fish price. The price paid to fishermen reflects the demand that exists among consumers for the different species of fish. In Nova Scotia the relative price for haddock, cod, and pollock is often approximately 3:2:1. This is the fundamental reason why the "causality" or "logic" of the Volterra–Lotka equations only exists for haddock. It is a "hunted species," while cod and pollock are often taken when it is difficult to obtain haddock, as by-catches or when inventories of these species fall to low levels. This is one reason why the understanding and control of a fishery cannot be based on single species equations or single spatial zones. Fishermen switch in and out of fisheries depending on the abundances available in others. As suggested by others (e.g. Mangel and Clark 1983), the relative profitability of fishing different species in different zones will be what drives fishing effort and generates the catch figures.

Simple Dynamic Model

As a first step towards unravelling this complexity, we have considered the haddock fishery in Division 4*X* and developed a simple program on a microcomputer to explore its dynamics. The equations take into account three age groups for fish, $X1 = 1 + 2$ yr olds, $X2 = 3 + 4$ yr olds, $X3 = 5+$ yr olds. We have used real numbers (in millions), weight at age, and the catch per boat required to keep it in the fishery. The following equations are used to model the haddock in Division 4*X* and the number of boat units actively fishing for haddock in this zone:

$$\begin{aligned}
dX1/dt &= bX3\,(1 - TX/N) - mX1 - S1X1Y - X1/T1 \\
dX2/dt &= X1/T1 - mX2 - S2X2Y - X2/T2 \\
dX3/dt &= X2/T2 - mX3 - S3X3Y \\
dY/dt &= RY(1 - C/(P(W1X1S1 + W2X2S2 + W3X3S3)) \\
dP/dt &= \mathrm{RR}\cdot P\,(1 - \mathrm{CA}\cdot P/\mathrm{MA})
\end{aligned} \tag{5}$$

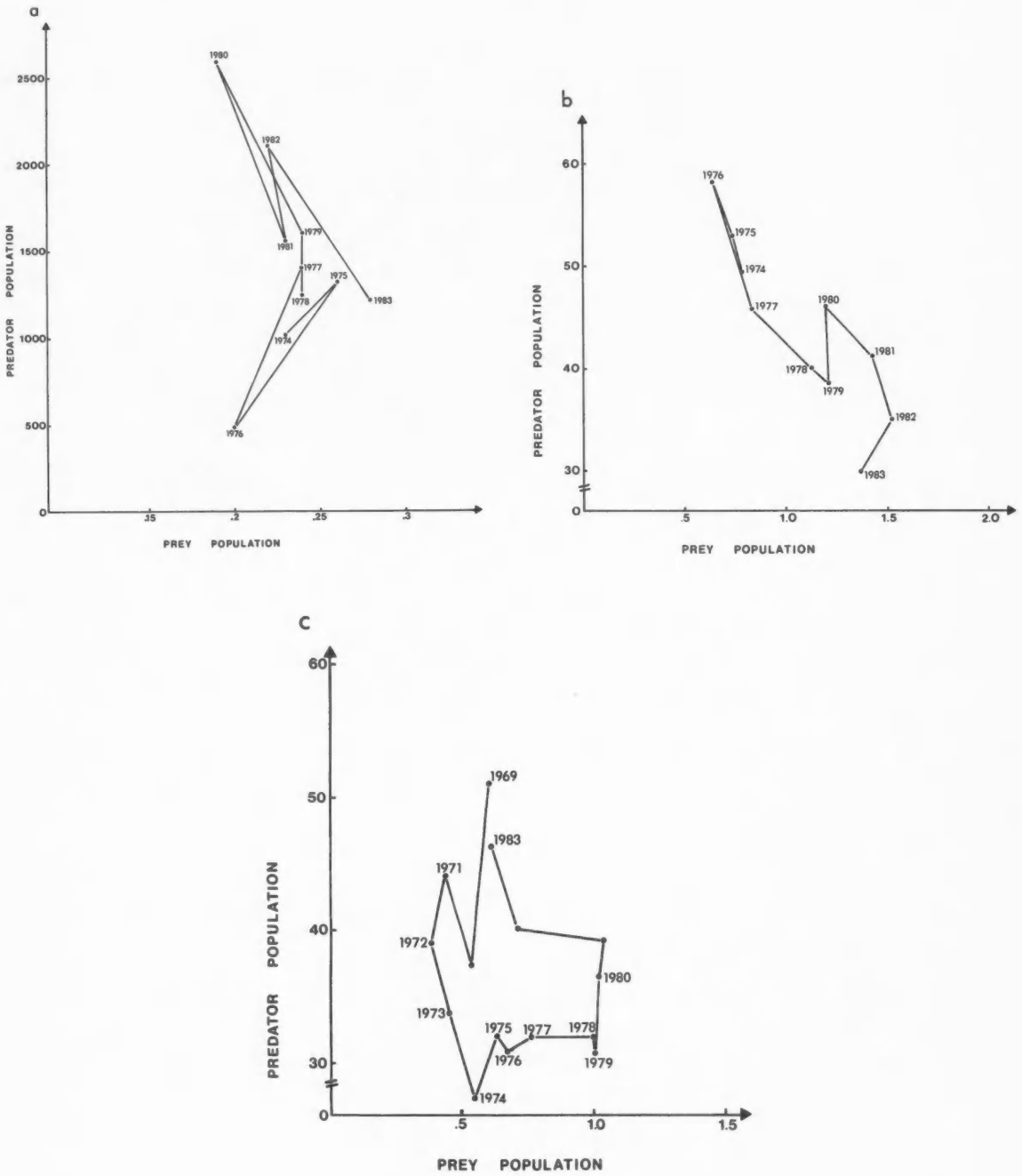

FIG. 4. Predator population (fishing effort) versus prey population (catch per unit effort) in NAFO Division 4X for (a) cod, (b) pollock, and (c) haddock.

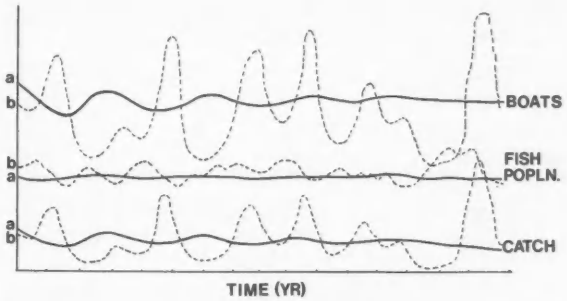

FIG. 5. Simulation results for the haddock fishery in NAFO Division 4X, supposing that the parameters of the equations can be represented by their mean values: *a*, deterministic approach to equilibrium; *b*, the average values of all the parameters are the same as for *a*, but now in each year the value of *b* is chosen to be good (1.45*b*), average (0.75*b*), or bad (0.05*b*) according to a random number. The system no longer goes to equilibrium, but instead executes fairly large, irregular oscillations which resemble reality.

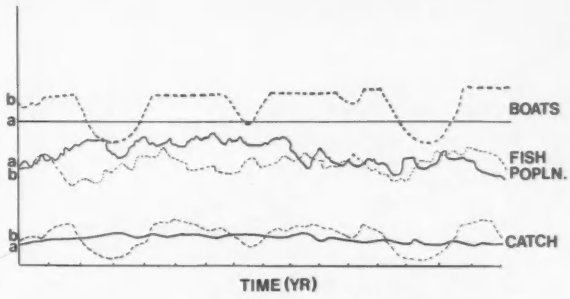

FIG. 6. Simulation results for the NAFO Division 4X haddock fishery showing the effects of limiting effort: *a*, with $y = 100$, we observe that at a slightly reduced yield, the system evolves for 80 yr without a major upset; *b*, with $y = 200$, we observe that in the long run one pays for the higher yield through more frequent crises. Policy exploration should be about attempting to find an acceptable balance between risk and yield.

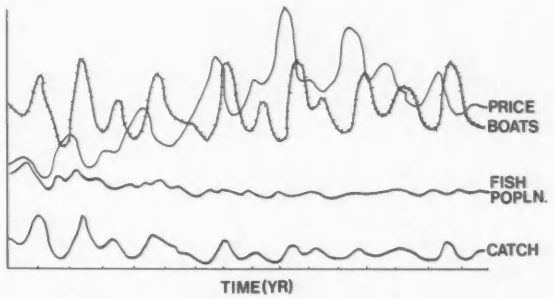

FIG. 7. Simulation results for the Division 4X haddock fishery in which the price of fish has been allowed to vary depending on supply and demand. Although this changes the evolution, it increases the number of crises. The effect of different rates of response and market elasticities can be examined using the model, and policy options can be explored taking into account the response of the market.

where b = birth rate, TX = total numbers of fish, m = natural mortality, $T1$ and $T2$ = time span of groups 1 and 2, $S1$, $S2$, and $S3$ = rate of capture between boats and fish at age, Y = number of boat units, R = rate of response of effort to profitability, $W1$, $W2$, and $W3$ = weight-at-age for $X1$, $X2$, and $X3$, C = revenue each boat wishes to make to maintain its effort, RR = rate of response of price to catch per unit time, P = price, CA = catch per unit time, and MA = market per unit time at unit price. These equations have a stationary state, and the saturation factor $(1 - TX/N)$ ensures that it is stable. Figure 5 (*a*) shows a typical deterministic simulation in which the values of $X1$, $X2$, $X3$, and Y and catch evolve in a damped oscillatory motion towards their stationary values. But it takes at least 70–80 yr to get near to equilibrium, and so the traditional fisheries management assumption that equilibrium always holds seems somewhat optimistic.

The model becomes more interesting when we add to the birth rate (b) a realistic amount of fluctuation around its average value. We use a random number each year to decide whether a year is good, medium, or bad (where good, bg = $1.45b$; medium, bm = $0.75b$; and bad, bb = $0.05b$), around the same average b. The result is dramatic (Fig. 5 (*b*)). The system amplifies the random fluctuations in b and sets itself into relatively violent and regular oscillations at approximately the Volterra– Lotka frequency.

It must be emphasized that the fluctuations which we have proposed for the haddock fishery are considered by fishery experts to be conservative, compared with reality. Turning off the fluctuations would give rise to a stationary state after some 70 or 80 yr, but in answer to the question, are cyclic crises in fisheries of natural or man-made origin, we suggest a new answer: *both*. Human responses amplify rapid random fluctuations and excite Volterra–Lotka type oscillations, but without the natural "noise" there would be nothing to amplify, and the fishery would be stable. This effect has in fact been observed in other fisheries such as for the north Californian dungeness crab (*Cancer magister*) (Botsford et al. 1983).

Our simple model has revealed a remarkable mathematical phenomenon: a system which normally would repose in a stable, stationary state can be set into a strong, characteristic oscillation with a particular frequency by the action of relatively rapid, random noise in the environment. This confirms a result presented at a workshop held in Texas, when Stucki and Horsthemke (1982) showed that a simple Volterra–Lotka system could be set in oscillation by environmental white noise. In their case, however, the stationary state was not truly stable, only of neutral stability. Our results confirm theirs, and go further by showing that stability in the deterministic system is no guarantee when environmental white noise is added. This line of research is being developed by Horsthemke and Lefever (1984), and we believe it to be of great interest for the understanding of natural and man-made systems.

Despite the simplicity of our model of equations (5), it offers management a useful tool with which to study the effects of certain policy decisions. Simulations presented in the Fig. 6 and 7 show the possible effects of different measures. For example, if fishing effort is limited to some upper level, there is a transition in the type of probability distribution underlying the fish population dynamics (Fig. 6 (*a* and *b*)). By putting a low upper limit on Y, we find a stable finite yield which never goes into crisis, despite various chance events in the fish dynamics. As this upper limit is raised, increasing short-term yield, successive crises occur at more and more frequent intervals until Y is "free" and cyclic disasters occur, with infrequent bursts of fish population rapidly fished out by an exaggerated effort.

This self-perpetuating, vicious circle represents just one possible regime in which the ecosystem could operate. Haddock, being high priced, are hunted ferociously, and therefore are rare, and high priced. Other species merely serve as financial stop-gaps when haddock are unobtainable. Other regimes with different species mixes, prices, and catches can also be explored by our model.

Dynamic, Multispecies, Multifleet Spatial Model

We now examine the fundamental ideas of "discovery" and "exploitation" which are at issue in the hunting of fish. We have constructed a dynamic multispecies model and applied it to the Nova Scotian groundfish fisheries. The model takes into account fishermen's decisions to switch species and fishing grounds according to their perceived relative opportunities. The equations (Appendix) describe the dynamics of fish populations in the different zones of the system as they spawn and multiply, and are then taken out of the system by fishing; the model can deal with up to four species of fish. The second set of equations describes the movement of fishermen, responding to information they have about catches being made by fleets fishing in the area. The model can describe the movements and behaviour of up to eight fleets and can trace the movement of fish and fishermen across some 40 spatial zones. Each boat is attracted to fish in a particular zone according to the relative attractivity of that zone as seen by the boat in question. Thus, the expected return that can be obtained from the reported catch and species mix in a zone is weighed against the cost of transferring to another zone, and the distance of that zone from the home port.

In constructing this "attractivity," we use the concept of "boundedly rational" decision making on the part of individuals. We suppose that the probability of an individual being attracted to a zone i, among all the others, is given by

$$P(i) = \frac{A_i}{\sum_i A_i}$$

where A_i is the attractivity of zone i. Since probability must vary from 0 to 1, A_i must always be defined as positive. A convenient form is

$$A_i = e^{IU_i}$$

where I is the quality of information and homogeneity of the population and U_i is a "utility function" and constitutes the "expected net rate of return" in zone i, taking into account the revenue from expected catch and the costs involved in obtaining that catch. These costs will take into account the distance d_{ij} from i to j and the fuel costs as well as the distance of zone i to port. In this representation the value of the parameter I determines the homogeneity of response between the different choices. If I is small, each choice will be made with equal probability, regardless of the real attraction of zones contained in the U_i. If I is large, even the smallest differences in real returns between the zones will lead to a single choice being made with 100% probability. Thus, I is related to "information exchanges" in the system.

When there are many individuals making choices, the fractioning of the population will reflect their relative attractivities. The population choosing i, y_i, from the total population y will be

$$y_i = y \frac{A_i}{\sum_i A_i}$$

with $A_i = e^{IU_i}$ as above.

With a population y perceiving and responding to the utilities U_i, the parameter I now reflects two factors: the "clarity" of information received and the homogeneity of the receiving population.

In our example, boats move between the different spatial zones of the system and the attractivity of any particular locality depends on where the boat concerned is situated. The fraction of boats of fleet L, situated at j, that is attracted by zone i is

$$y_i^L \cdot \frac{A_{ij}^L}{\sum_i A_{ij}^L}$$

and the total number attracted to i from all the possible j's is

$$y^L p_i = \sum_j y_j^L \cdot \frac{A_{ij}^L}{\sum_i A_{ij}^L} = (\text{potential } y_i^L).$$

The movement of boats around the system is therefore generated by the difference at a given time between $y^L p_i$ and y_i^L, the number of boats *actually* in i. If $y^L p_i$ is greater than y_i^L, boats will move into i from other zones. If $y^L p_i$ is less, they leave. They move at a *finite* rate depending on the rapidity with which they are willing and able to react. As they travel to different zones to fish, the relative attractivities of the zones are modified. Once this is detected, further response on the part of the fishing boats results in new patterns of fishing effort, with continuous dynamic movement of boats and fish resembling, when calibrated, that of the real system.

One of the many possible areas of interest opened up by such a model is the examination of different spatial strategies, and what we have called "the dynamics of discovery and exploitation." For hunted species, the yield will depend on "locating" aggregations of prey and then mobilizing and directing fishing effort to this location. This objective can be achieved in different ways: either an "unstructured" population of "generalist" fishermen who do both functions, or various structured possibilities involving "risk taking" skippers who are specialized in "discovery" and others who only go to locations where present information tells them the "highest returns" can be found. This structured organization requires information exchange between the different types of fisherman. To handle this in our model, we have considered that the "expected return" from fishing in a zone i that influences the U_i^L of attractivity will be "channelled" between fleets or types according to an "information exchange" matrix. Thus, the "expected catch" in a zone for a particular fleet or type is generated by total information received from other vessels of the same and other fleets. The concept of "information exchange," of lying or speaking in codes to one's own fleet is expressed in the term

$$\text{Expected catch} = \sum_{L'} \epsilon^{LL'} \left[\sum_k \left[\frac{p^k w^k \cdot s x^k y^{L'}}{(1+s)^\tau \left(\sum_k x^i \right)} \right] \cdot \frac{1}{(1 + 0.3 y^{L'})} \right]$$

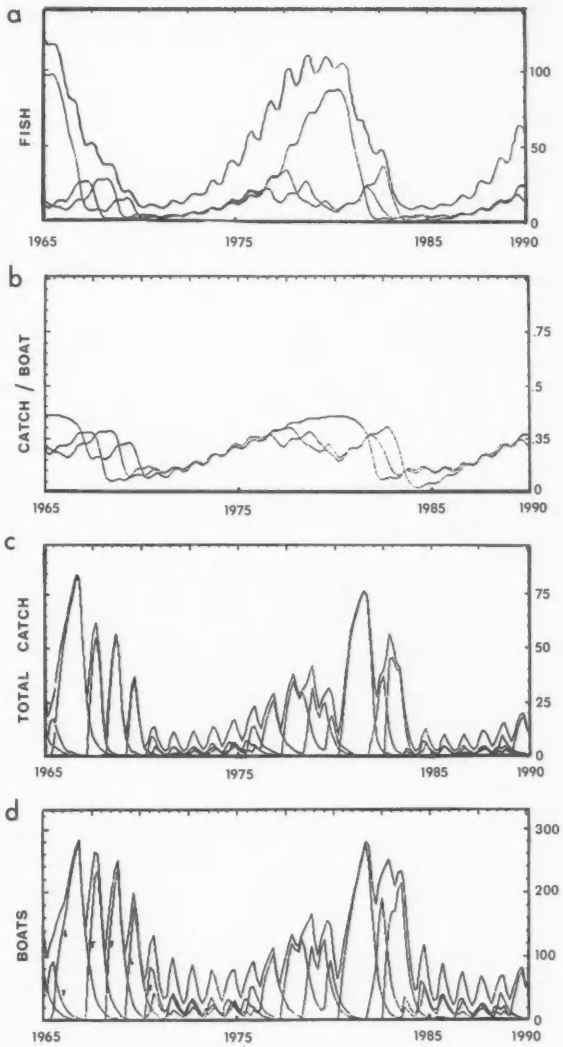

FIG. 8. Simulation of the haddock (*Melanogrammus aeglefinus*) fishery in Division 4X: (a) fish population; (b) catch/boat; (c) total catch; (d) boat units.

where L' = index of fleet type, k = indicates the species of fish, w^k = the average weight, p^k = price per kilogram of the species k, and τ = time for boat to handle 1 unit of x (where x = 1000 t). The epsilons describe the reception of catch information. The term at the end $(1/(1 + 0.3y^{L'})$ makes the term sensitive to catch per boat instead of just catch as the number of boats increases.

Thus, vessels play a dual role when fishing: they "exploit" the zone they happen to be in, and they sample local conditions and transmit the information to chosen associates.

This model is still under development, but we shall present some of the preliminary studies we have made, and which give rise already to some interesting points. In Fig. 8a–8d we show the results generated by a simple version involving only one fleet and one fish species, with three fishing grounds situated

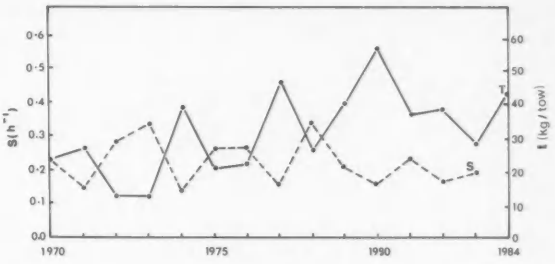

FIG. 9. Ease with which fishermen locate fish (S) (catch rate/abundance) and fish abundance (t) over time for haddock in Division 4X, where abundance is derived from research vessel survey estimates.

100 km from the home port. The simulation starts with the approximate figures for haddock in NAFO Division 4X in 1965 and runs forward to 1990. It corresponds fairly well to observation for the period 1965–84, and this must unfortunately lend some credibility to the continued evolution until 1990. Leaving aside this practical question of "prediction," what the simulation also shows is the importance of "fishermen's knowledge" in generating the catch figures observed. The catch and effort figures for the three zones *aggregated* cannot be easily interpreted, since at various moments fishing effort can be misdirected to zones where fish are less abundant. This shows that in an inhomogeneous system such as the real world, aggregation of data over inhomogeneities can lead to changes in the apparent "catchability" of fish as boats home in on high abundances. In this example, a hunted species of fish gives rise to a situation where fish abundance (x indicated by t per tow) and the ease with which fishermen locate the fish (S) (catch rate/abundance) change over time out of phase (Fig. 9). This is because as fish density increases aggregates generally form, but they must first be discovered by fishermen before effort can be channeled to their exploitation, and boats will fish in the "right places." Thus, initially, t increases and S drops. Once discovery has occurred, effort is directed to the dense aggregates and fish abundance drops, while S increases. This turns out to be the case for haddock in Division 4X where independent estimates of fish abundance can be made from research vessel data. It also applies in our model of the haddock fishery in Division 4X. But is is not found for cod or pollock in Division 4X. There is no "out of phase relationship" between abundance and the apparent value of S. This supports the validity of our fundamental hypothesis that only haddock is really hunted in Division 4X. Cod and pollock are only taken as a stop-gap when haddock is rare, and so finding these species is not the main limiting factor on their catch. In this way the model helps to unravel some of the misleading information contained in the commercial catch data, which a nonspatial approach would fail to reveal. It is partly these misconceptions concerning the "apparent" abundance of fish derived intuitively from catch data that allows a "managed" fishery to continue to suffer cyclic crises despite the best efforts of managers.

Another significant result that the model generates concerns the "discovery" and "exploitation" mechanisms and the questions of information exchange, rationality, and randomness. Other important considerations are superimposed on the basic spatial movements towards the aggregates of high priced fish at the nearest locations. For example, skippers whose behaviour is only weakly influenced by this information, who either

TABLE 1. Number of boats in stochastic fleet (Bs) and in cartesian fleet (Bc) under different conditions of I, the quality of information and homogeneity of the populations (Is and Ic), and with varying information matrices (a = information within the stochast fleet; b = information from cartesian fleet to stochast fleet; c = information from stochast fleet to cartesian fleet, d = information within the cartesian fleet). Price of fish species F_2 is three times F_1.

	Information matrix $\begin{pmatrix} a & b \\ c & d \end{pmatrix}$											
	$\begin{pmatrix} 1 & 0.5 \\ 0.5 & 1 \end{pmatrix}$		$\begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix}$		$\begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix}$		$\begin{pmatrix} 1 & 0 \\ 1 & 1 \end{pmatrix}$		$\begin{pmatrix} 1 & 1 \\ 0 & 1 \end{pmatrix}$		$\begin{pmatrix} 1 & 0.1 \\ 0.1 & 1 \end{pmatrix}$	
I_s	0.2		0.2		0.5		0.2		0.2		0.2	
I_c	2.0		2.0		2.0		2.0		2.0		2.0	
Time (yr)	Bs	Bc	Bs	Bc	Bs	Bc	Bs	Bc	Bs	Bc	Bs	Bc
1	62	50	61	50	62	50	61	50	62	50	61	50
2	83	68	85	67	83	67	85	69	83	67	84	67
3	114	93	119	83	89	72	114	95	116	79	116	92
4	149	122	160	92	97	55	150	126	137	82	150	118
5	189	156	225	85	139	34	191	161	228	74	192	150
6	238	196	290	69	183	22	237	200	296	59	241	185
7	270	229	371	50	186	16	269	236	382	45	275	209
8	283	251	424	34	185	13	281	256	432	31	294	222
9	258	236	448	23	192	12	253	239	457	21	276	218
10	217	210	438	18	263	12	209	210	445	17	242	185

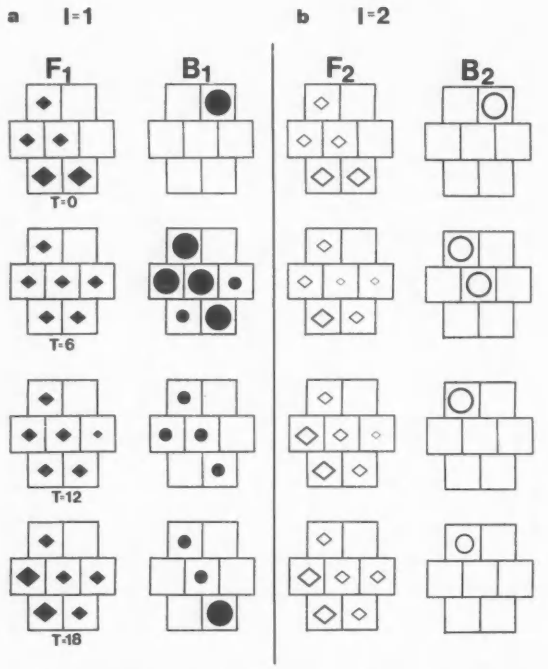

FIG. 10. Simulation results from a 15-yr run of one species of fish (F) and one fleet type (B) with ($T/1.2$ = yr): (a) I = 1, and F_1, B_1; (b) I = 2 and F_2, B_2.

search "randomly" or according to some personal scheme of knowledge, will be characterized in our model by a small I. We will call them *stochasts*. At the other extreme we have skippers who, for various reasons, are unwilling to take any risk and will go to the zone promising the best *known* return, no matter how low, as long as it is certain. We shall call them *cartesians*. They will be characterized by a larger value of I.

To demonstrate the effects of I, we compare two simulations performed under identical conditions, except that in one case we set I = 1 and in the other I = 2. When I = 1 (Fig. 10a) the fleet discovers the various zones of high return and travels to successive areas, fishing out high paying aggregates. There is a period when stocks must recuperate, but basically the fishery continues, with "search" and "discovery" occurring over the whole area, leading to a typical series of good and bad years as observed in reality.

Figure 10b shows the long-term evolution of the fishery if I = 2. Over time this is disasterous, although in the short term it simply directs boats rather clearly to the "best" zone for fishing. The information about which is the best zone is generated only by boats which are fishing, and there is a kind of "locking" onto one particular location with a shut down of "random" sampling. In the long run this leads to the fishery simply exploiting a single location instead of the whole area, with a small catch and small fishing fleet. In contrast, I = 1 results in the maintenance of fishing activities over the whole area of the system and a much higher catch and larger fishing industry. Thus, less "information" allows a more "fuzzy" or "random" response on the part of boats, meaning that they continue to explore the less visited parts of the system. In a way they take more risks, but the result is that the system survives instead of virtually shutting down. If boats refuse to take risks and go only to where they know for sure that there are some fish, the end result is disaster. Discovery must involve risk. But to abandon discovery is in reality to make disaster certain.

In the next series of simulations we again explore the effect of having the two types of fishermen, stochasts and cartesians, and test their relative and combined effectiveness for different conditions of information exchange: the results are shown in Fig. 11a–11f and summarized in Table 1. Figure 11a shows 10 yr of evolution for a situation in which catch information is passed between stochasts (I = 0.2) and cartesians (I = 2.0) at 0.5 the rate it is within each type. Over the initial period, the stochasts are more successful than the cartesians, keeping ahead by discovering aggregates quicker than the others. In the later period when fish stocks have declined, the two strategies do almost equally well.

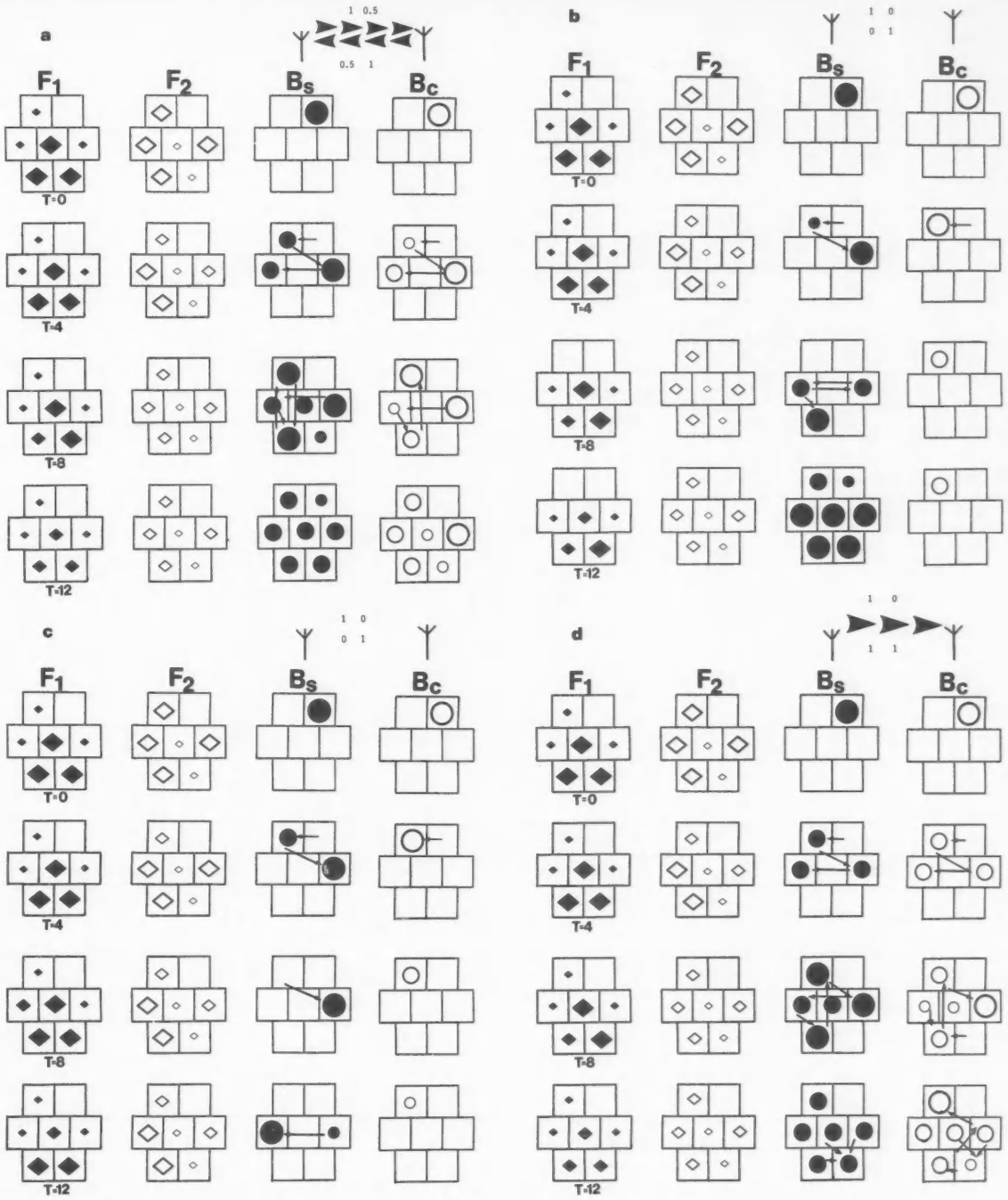

FIG. 11. Simulation results over 10 yr ($T/1.2$ = yr) with two fish species, F_1 and F_2, and two fleet types, Bs (stochast fleet) and Bc (cartesian fleet). F_2 is three times the price of F_1. The size of the symbols is relative and particular to each run; thus, they are used simply to indicate very small (approximately less than 10), medium, and large quantities. The numbers in the information matrix $\begin{pmatrix} a & b \\ c & d \end{pmatrix}$ refer to exchange of information and are keyed as follows: a = information flow within the stochast fleet, b = information flow from cartesian fleet to stochast fleet, c = information flow from stochast fleet to cartesian fleet, d = information flow within the cartesian fleet. (a) $I_s = 0.2$, $I_c = 2$, and partial information exchange (0.5) between fleets; (b) $I_s = 0.2$, $I_c = 2$, and no exchange between fleets; (c) $I_s = 0.5$, $I_c = 2$, and no exchange between fleets; (d) $I_s = 0.2$, $I_c = 2$, and no information flow from cartesians to stochasts; (e) $I_s = 0.2$, $I_c = 2$, and no information flow from stochasts to cartesians; (f) $I_s = 0.2$, $I_c = 2$, and small level (0.1) of information flow from stochasts to cartesians. (*Fig. 11 concluded next page*)

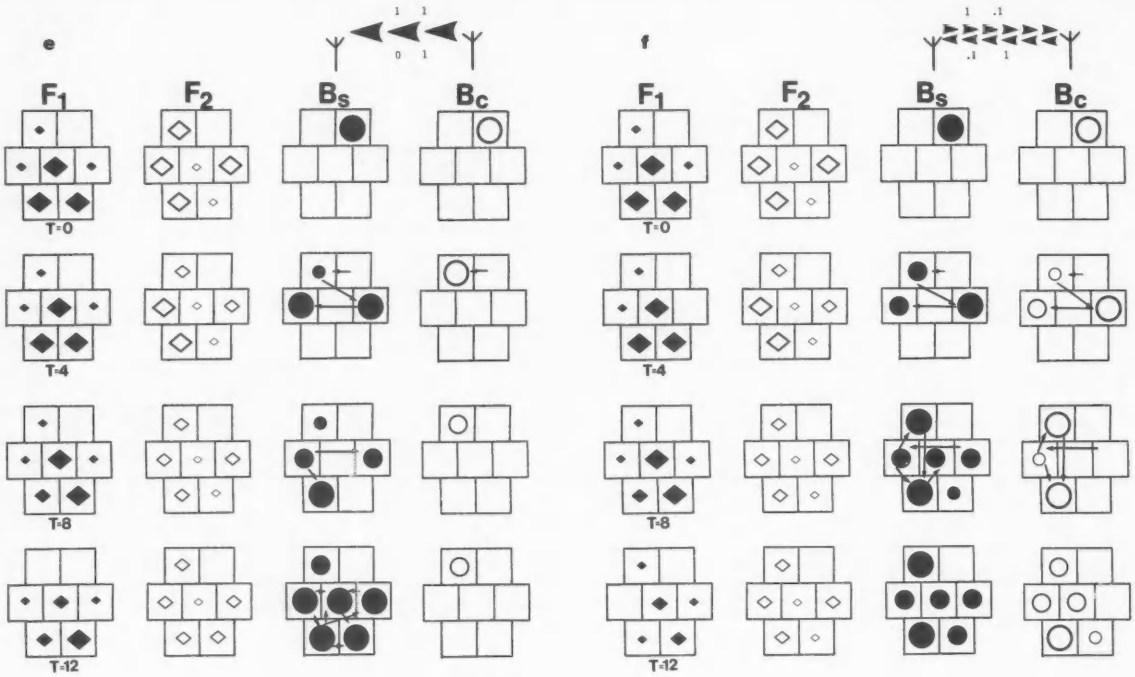

FIG. 11. (*Concluded*)

The second case shows how the stochasts act as the "eyes" of the fishing fleets. If, however, the information they have is not transmitted to the others, then the system as a whole does not exploit the resource very efficiently. The cartesians, starved of information about fresh discoveries, simply wither away, fishing out the one zone that they have discovered (Fig. 11b). The only surviving strategy is that of the stochasts, but this is not necessarily effective at concentrating effort strongly in the zones where large aggregates have been located. A similar phenomenon is found when stochasts have a higher value of I, and remain much more bunched (Fig. 11c).

These conclusions are reinforced by Fig. 11d and 11e, which show what happens when either the cartesians or the stochasts cheat by not transmitting information about their catches. There is an interesting asymmetry. If the cartesian fails to inform the stochast, then it has very little effect, while if the situation is reversed, the cartesians perish, leaving the field free to stochasts. Therefore, a natural reaction for cartesians will be to *try* to obtain information, while the others will simply attempt not to give it. This has resulted in the evolution of "listening in" on radios, of coded messages, of "lying," "misinformation," etc.

Figure 11f, incorporates another source of structural complexity: an explanation of the baroque of the real world. Here, we suppose a very weak mutual exchange of information. This is very effective globally. The stochasts locate aggregates and direct very concentrated fleets of cartesians to the relevant locations. The possibility of such efficiency means that a natural evolution would be to have in each competing fleet a subdivision of "researchers" and "producers" so that they cooperate within a fleet, but not with competing fleets. The immense richness and apparent obtuseness of much of human behaviour can be better understood in terms of such a model. In large fishing fleets, this type of complicity is indeed present, since the managers persuade their best captains to go off in search of new fishing grounds by promising them in return a trip to a highly profitable area as a reward.

In the Nova Scotian situation there are two types of fishermen: those who are "average" and those who are called "highliners." The latter are adventurers who take risks, discovering new concentrations of fish and always leaving areas in search of further discoveries before they are completely fished out. There is a population of "risk takers" and a population of "imitators." Risk takers happen to earn significantly more money than the others by their strategy, and this enables them to take risks. This is another example of a self-perpetuating situation, where a successful highliner ensures his continued ability to operate as a highliner, by being able to afford better equipment, and withstand small periods of "bad luck." An "imitator" must have both determination and good luck if he is ever to make the transition. This is an evolutionary mixed strategy, where it is the complementarity of two behaviours that ensures reasonable exploitation of a resource.

General Discussion

In the preceding sections we have tried to show that new concepts emerging from dissipative structures and nonlinear systems give rise to models which can be usefully applied to the understanding and management of fisheries. We feel that these ideas are of great generality and should enable some wider conclusions to be drawn.

A number of important points have been raised. First, when faced with the problem of understanding a complex system, it

is vital to identify the "actors" in that system and to include explicitly their responses and actions in the model. The "subjective" views of each actor must be taken into account rather than supposing that some global principle, such as "optimal" efficiency or an equilibrium state, can be invoked. Such assumptions are clearly dubious in the real world where we are most often faced with dynamical systems composed of individuals, each of whom is trying to attain his ends and who is doing so on the basis of information which is constantly being gained and lost as the system changes.

The second point concerns fluctuations. They are not simply a "nuisance," a perturbation of average results, but instead are the motor of evolutionary change and explain the very "nature" of many systems. In the case of our fishery example the feedback responses of the human system are such that they amplify the yearly random fluctuations of the environment, and generate large, fairly regular cycles of boom and bust, despite the fact that the deterministic system has a stable equilibrium solution.

The third issue is that of the importance of calibration of these types of models. In our case study it has been possible to use realistic figures and parameters, so that the phenomena discussed and predicted are of relevance to the real world. It is harder for industries and practitioners to ignore a model that deals with real numbers, since then the intuitions and prejudices of decision makers require justification. The real use of such models must be as a "learning tool" rather than as a *predictive* instrument. They enable us to understand the part of the evolution of a system which may be due to the mechanisms contained in the model, and suggest when additions are necessary to understand the behaviour of the evolving and creative world in which we live. They also allow decision makers to explore the possible implications of proposed actions before putting them into effect, and can be used to better "imagine" the future, and to suggest other ways of doing things. Our ideas are therefore very close to those of Holling (1978) in this respect, viewing "management" as an on-going process, where we continue to adapt our ideas and models to the evolving situation.

The final point we raise is probably the most important. It concerns the question of "discovery," of evolutionary survival, and of information exchange. There is a fascinating parallel between the picture we have derived concerning fishing behaviour and that revealed by recent research into foraging behaviour in the animal kingdom, particularly in work on ant societies (Deneubourg et al. 1983). The vital issue is that "discovery" like "invention" and "creation" can be achieved through "nonrational" behaviour, although subsequent exploitation may depend on "rational" reactions. The multifacetted process of "discovery" and "exploitation" concerns all of us at many levels. Either as individuals or in our various roles in families, firms, institutions, communities, and even nations, we must try to decide how to divide our time and effort between the performance of tasks characteristic of our present role, with known values and pay-offs, or the continued search for, and openness to, the possibilities of new roles and new pay-offs in the future.

As individuals we can either deliberately allow ourselves to explore new paths and connections, or instead, we can organize most of the components of our lives so that we minimize such diversions which, at any given moment, have no obvious purpose. There are again two extremes: "stochasts" and "cartesians." The former take intellectual, emotional, or financial risks by adventuring into the unknown, be it with ideas, aesthetics, personal relationships, or entrepreneurial activities. Their discoveries are what nourishes society in the long run, and assures its survival by allowing to to evolve, and to find new sources of sustenance. The latter devote themselves to fulfilling as efficiently and completely as possible the role they feel has been assigned to them. Their behaviour constitutes the "backbone" of society, and offers a very necessary definition of "normality." The successful, long-term functioning and survival of an individual, a society, a firm, or a nation requires both types of behaviour, just as our example dealing with "fishing" showed.

These wider aspects of human behaviour, illustrated and brought to light by our model of fishing, with its complementary tasks of "discovery" and "exploitation," will be the object of further study. The whole question of "innovation" and of management can be examined in terms of these new ideas. Old views of policy and planning as a "rationalization," and classification, streamlining, and separation of different functions must be reexamined. We need to design systems which are capable of being creative, not imposing too much rationality or too much information on them. Neither should we restrict movements or thoughts to only the known or recognized channels characterized at present by an obvious usefulness. Discovery requires freedom, while the efficient functioning of society requires cooperativity and organization. Perhaps with models such as ours, we can begin to understand and explore a new "rationality" which encompasses both harmoniously.

As Confucious said, "Give me a fish and I eat today, but teach me *how* to fish and I shall never be hungry." If we can discover *how* to fish, then we shall indeed have taken a large step forward.

Acknowledgments

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References

BEDDINGTON, J. R. 1979. Harvesting and population dynamics, p. 307–319. *In* R. M. Anderson, B. D. Turner, and L. R. Taylor [ed.] Population Dynamics. The 20th Symposium of the British Ecological Society, London, 1978. Blackwell Scientific Publications, Oxford.

BEDDINGTON, J. R., AND R. M. MAY. 1977. Harvesting natural populations in a randomly fluctuating environment. Science (Wash., DC) 197: 463–465.

BEVERTON, R. J. H., AND S. J. HOLT. 1957. On the dynamics of exploited fish populations. U.K. Minist. Agric. Fish. Invest. (Ser. 2) 19: 1–533.

BOTSFORD, L. W., R. D. METHOT JR., AND W. E. JOHNSTON. 1983. Effort dynamics of the northern California Dungeness crab (*Cancer magister*) fishery. Can. J. Fish. Aquat. Sci. 40: 337–346.

CADDY, J. F. 1983. An alternative to equilibrium theory for management of fisheries. World Conference on Fisheries Management and Development, F.A.O., WCFMD/Prep. 1 Sess. 2./Panel 2.2.

DENEUBOURG, J. L., J. M. PASTEELS, AND J. C. VERHAEGHE. 1983. Probabilistic behaviour in ants: a strategy of errors? J. Theor. Biol. 105: 259–271.

DOUBLEDAY, N. G. 1976. Environmental fluctuations and fisheries management. ICNAF Sel. Pap. 1: 141–150.

HOLLING, C. S. [ED.] 1978. Adaptive environmental assessment and management. International Series on Applied Systems Analysis. Wiley Interscience, John Wiley & Sons, New York, NY.

HORSTHEMKE, W., AND R. LEFEVER. 1984. Noise-induced transitions. Theory and applications in physics, chemistry, and biology. Springer Series in Synergetics, Vol. 15. Springer-Verlag, New York, NY. 318 p.

JONES, D. D., AND C. J. WALTERS. 1976. Catastrophe theory and fisheries regulation. J. Fish. Res. Board Can. 33: 2829–2833.

KIRBY, M. J. L. (CHAIRMAN). 1982. Navigating troubled waters: a new policy for the Atlantic fisheries. Report of Task Force on Atlantic Fisheries. Canadian Government Publishing Centre, Ottawa, Ont.

MANGEL, M. 1982. Search effort and catch rates in fisheries. Eur. J. Oper. Res. 11: 361–366.

MANGEL, M., AND J. BEDER. 1985. Search and stock depletion: theory and applications. Can. J. Fish. Aquat. Sci. 42: 150–163.

MANGEL, M., AND C. W. CLARK. 1983. Uncertainty, search and information in fisheries. J. Cons. Int. Explor. Mer 41: 93–103.

MAY, R. M., J. R. BEDDINGTON, C. W. CLARK, S. J. HOLT, AND R. M. LAWS. 1979. Management of multispecies fisheries. Science (Wash., DC) 205: 267–277.

MCGLADE, J. M., AND P. M. ALLEN. 1985. The fishery industry as a complex system, p. 209–216. *In* R. Mahon [ed.] Towards the inclusion of fishery interactions in management advice. Can. Tech. Rep. Fish. Aquat. Sci. No. 1347: 221 p.

NICOLIS, G., AND I. PRIGOGINE. 1977. Self-organization in nonequilibrium systems: from dissipative structure to order through fluctuations. Wiley Interscience, John Wiley & Sons, New York, NY. 491 p.

NISBET, R. M., AND W. S. C. GURNEY. 1982. Modelling fluctuating populations. Wiley Interscience, John Wiley & Sons, New York, NY. 379 p.

PEARSE, P. H. 1982. Turning the tide: a new policy for Canada's Pacific fisheries. The Commission on Pacific Fisheries Policy, Vancouver, B.C.

PRIGOGINE, I., AND P. M. ALLEN. 1982. The challenge of complexity, p. 3–39. *In* W. C. Schieve and P. M. Allen [ed.] Self-organization and dissipative structures. Applications in the physical and social sciences. University of Texas Press, Austin, TX.

SISSENWINE, M. P. 1984. Why do fish populations vary?, p. 59–94. *In* R. M. May [ed.] Exploitation of marine communities. Dahlem Konferenzen, Springer-Verlag, Berlin.

STUCKI, J. W., AND W. HORSTHEMKE. 1982. Creation of order by environmental noise in the Volterra–Lotka model, p. 187–192. *In* W. C. Schieve and P. M. Allen [ed.] Self-organization and dissipative structures. Applications in the physical and social sciences. University of Texas Press, Austin, TX.

Appendix: Equations of the Multispecies, Multifleet Spatial Model

The differential equation governing the change in population of the fish k, at point i, is

$$\frac{dx_i^k}{dt} = b^k x_i^k (1 - x_i^k/N_i) - \sum_L \frac{s x_i^k y_i^L}{\left(1 + s\tau \sum_k x_i^k\right)}$$

The equation governing the change in numbers of vessels of fleet L at point i is

$$\frac{dy_i^L}{dt} = \xi \left(\sum_j \frac{y_j^L A_{ij}^L}{\sum_{i'} A_{i'j}^L} - y_i^L \right) + r y_i^L \left(1 - C_i \Big/ \sum_k \frac{s x_i^k}{\left(1 + s\tau \sum_k x_i^k\right)} \right)$$

where x_i^k = fish population of type k at i, y_i^L = boat numbers of fleet L at point i, b^k = rate of natural increase of species k, N_i = natural carrying capacity of the point i, s = rate of interaction between fish and boats, τ = time for a boat to handle 1 unit (1000 t) of x, ξ = mobility of the boats, r = rate of response of effort to profitability, C_i = cost of fishing at i, A_{ij}^L = attractivity of i, to L, viewed from j, $A_{ij}^L = \exp(IU_{ij}^L)$, U_{ij}^L = utility function (as described in text) or "expected net rate of return" in zone i viewed from j by a boat in fleet L, taking into account the revenue from expected catch, the costs involved in obtaining that catch $\theta(d_{ij} + d_{ip})$, and the information flow matrix $\epsilon^{LL'}$ between fleet types L' and L, I = quality of information and homogeneity of the population, θ = fuel cost per unit distance, d_{ij} = distance from i to j, and d_{ip} = distance from i to port.

Phosphorus Release Processes in Nearshore Southern Lake Michigan[1]

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Quigley, M. A., and J. A. Robbins. 1986. Phosphorus release processes in nearshore southern Lake Michigan. Can. J. Fish. Aquat. Sci. 43: 1201–1207.

We determined soluble reactive phosphorus (SRP) release rates from intact, medium-fine sand cores obtained from an 11-m-deep sampling site in nearshore Lake Michigan during July–October 1980. Mean SRP release ranged from 0.17 ± 0.03 (SE) to 0.57 ± 0.04 mg PO_4-P·m^{-2}·d^{-1}. Pore water analysis indicated that, despite high dissolved oxygen concentrations in the uppermost 6 cm of sediment, SRP concentrations increased rapidly with depth throughout this zone. Moreover, a Fickian diffusion equation based on the SRP pore water gradient and physical sediment features predicted a release rate (1.12 mg PO_4-P·m^{-1}·d^{-1}) that was 2–7 times higher than release rates measured from intact cores. Results suggest that nearshore sediments provide a ready pathway for the return of SRP to overlying water, and this process warrants inclusion in future conceptual models of Lake Michigan's phosphorus cycle.

Nous avons déterminé, de juillet à octobre 1980, les taux de passage en solution du phosphore réactif soluble (PRS) dans la zone littorale du lac Michigan. L'étude portait sur des carottes de sable intactes de granulométrie moyenne-fine prélevées à 11 m de profondeur. Le taux de passage du PRS variait de 0,17 + 0,03 (ET) à 0,57 + 0,04 mg·m^{-2}·d^{-1} de PO_4-P. L'analyse de l'eau interstitielle a montré que les concentrations de PRS augmentaient rapidement avec la profondeur tout au long de cette zone, ceci en dépit de teneurs élevées en oxygène dissous dans les 6 premiers centimètres de sédiments. De plus, une équation de diffusion de Fick bassée sur le gradient du PRS des eaux interstitielles et les caractéristiques physiques des sédiments prévoyait un taux de passage en solution (1,12 mg·m^{-2}·d^{-1} de PO_4-P) qui était de 2 à 7 fois supérieur aux taux déterminés à partir des carottes intactes. Il semble, sur la base de ces resultats, que les sédiments de la zone littorale permettent facilement au PRS de repasser en solution dans les eaux sus-jacentes. Nous croyons qu'il est justifié d'inclure ce processus aux modèles conceptuels du cycle du phosphore qui seront élaborés pour le lac Michigan.

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Phosphorus availability has been closely linked to primary production rates and accelerated eutrophication in the Great Lakes (Dillon and Rigler 1974). As a result, a thorough understanding of lakewide phosphorus dynamics is needed to devise cost-effective strategies that forestall declines in water quality. In particular, phosphorus exchange between sediments and lake water has been widely recognized as an important phosphorus cycling pathway (Mortimer 1941, 1942; Lee 1970). Although aerobic sediments have been traditionally viewed as a phosphorus sink, with phosphorus sorbing to Fe, Mn, or Al oxide–hydroxide complexes (Syers et al. 1973), a number of studies have described significant phosphorus release from oxic sediments (Lee et al. 1977; Neame 1977; Bannerman et al. 1974). This aerobic phosphorus release has most frequently been attributed to physical and metabolic interactions between resident macroinvertebrate fauna and sediments (Gallepp 1979; Holdren and Armstrong 1980; Neame 1977; Graneli 1979; Gardner et al. 1981). In the Great Lakes, where aerobic sediments predominate (Mortimer 1971), these animal–sediment interactions may constitute an important pathway of phosphorus regeneration to overlying water. At present, however, the overall significance of sediment phosphorus regeneration within lakewide phosphorus budgets is largely unknown. In Lake Ontario, Bannerman et al. (1974) estimated that phosphorus flux from aerobic sediments was about 10% of the external annual phosphorus loading.

The primary objective of our study was to measure the flux of soluble reactive phosphorus (SRP) between sediments and overlying water of intact Lake Michigan cores. By subsequently comparing SRP flux in individual cores with corresponding abundances of major macroinvertebrate groups, we sought to isolate possible effects of animal–sediment interactions on SRP exchange.

Our investigations focused on nearshore Lake Michigan, an area that has high phosphorus loading from tributaries and water quality that is consequently different from offshore waters (Schelske 1980). This area is defined by Mortimer (1975) as a 10-km-wide coastal zone where water depth is generally less than 30 m and where the effects of wave and current action on sediments are concentrated. Because water resource use occurs primarily in nearshore areas, future water quality management strategies must include a basic understanding of the phosphorus cycle in this zone.

[1]GLERL Contribution No. 427.

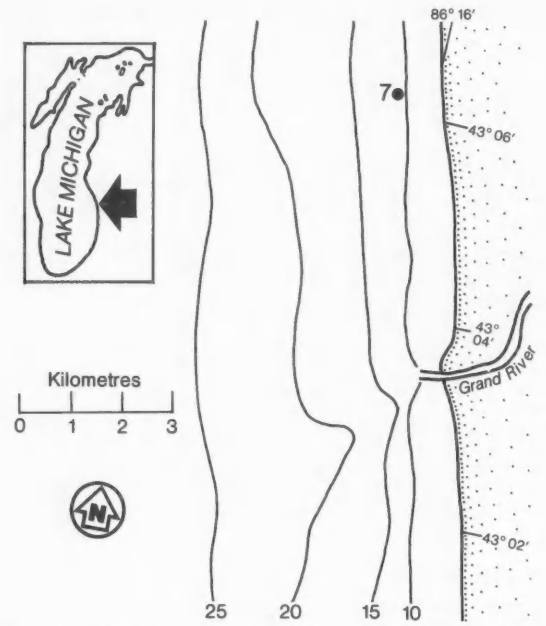

FIG. 1. Location of study site (Station No. 7) in nearshore southeastern Lake Michigan.

Methods

Study Site

Sampling was carried out in the southeastern Lake Michigan nearshore zone at a site 11 m deep located 1.0 km offshore and 5.5 km north–northwest of the mouth of the Grand River (86°17′00″W, 43°06′18″N; Fig. 1). Surface deposits in this area bore ripple marks and irregular contours, indicating wave and current activity. However, a thin (0.5–3 mm) surficial floc layer of clay/silt-sized particles was present throughout spring and summer (Nalepa and Robertson 1981). Thus, bottom turbulence was sufficiently low to allow this easily resuspended material to remain at the sediment–water interface during these periods. At other times, the material was eroded and transported to deeper regions of the lake (Chambers and Eadie 1980; Eadie et al. 1979).

Underlying sediments at the site consisted of well-sorted, medium-fine beach sand with a median particle size of 1.9 ϕ (270 μm) (Quigley and Robbins 1984). Sediment porosity (Fig. 2) declined with depth from 50.2 ± 19.4% (SD) in the uppermost 1 cm layer to 31.5 ± 2.9% at a depth of 6.5 cm (Quigley and Robbins 1984).

Vertical concentration profiles of dissolved oxygen and SRP in pore waters were determined by use of three sediment peepers (Hesslein 1976). Each sampler had a series of five compartments containing filtered lake water separated from surrounding sediments by a 0.45-μm polycarbonate membrane. Water was stripped of oxygen by vigorous nitrogen bubbling prior to filling of the peepers, and peepers were held in oxygen-free water within a closed container that was opened only once, immediately before divers deployed the devices in the sediments. Peepers were deployed in sediments in July and withdrawn in September (53 d deployment interval). They were retrieved by first attaching a line and then rapidly hauling them

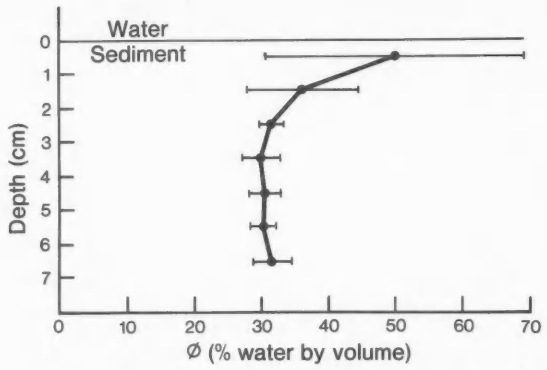

FIG. 2. Sediment porosity (ϕ) versus depth below sediment–water interface from 18 cores collected at the study site from May to October 1979 (on six sampling dates, three cores per date).

onboard where they were immediately stored under mineral oil at 4°C to prevent contamination by atmospheric oxygen. Oxygen and phosphorus concentrations of water in peeper compartments were determined 1–2 h later. A modified (Azide) microwinkler method (Fox and Wingfield 1938) was used to measure dissolved oxygen concentrations. SRP concentrations (expressed as micrograms PO_4-P per litre) were determined by the ascorbic acid method (American Public Health Association et al. 1976).

Core Collection and Incubation

A total of 35 intact (diver-collected) cores were taken on three 1980 dates: July 24 (16 cores), September 8 (6 cores), and October 5 (13 cores). Cores tubes were 4.5 cm in diameter with an overall length of 30 cm. Tubes were inserted into sediments to a depth of 10 cm and then stoppered at both ends prior to removal. Cores were transported to a dockside laboratory, where they were incubated in darkness at 12°C. Filtered air was bubbled through overlying water to promote mixing and to prevent any vertical SRP gradient from forming above the sediment–water interface. This experimental arrangement was intended to simulate turbulent current regimes in the benthic boundary region of the nearshore environment where, presumably, a stagnant layer does not exist. Aeration also held dissolved oxygen concentration in overlying water at levels greater than 90% saturation.

Cores and aeration lines used in experiments were composed of high-density linear polyethylene to minimize SRP adsorption which is known to bias SRP flux measurements (Holdren and Armstrong 1980). Cores showing evidence of water leakage were not included in SRP estimates.

SRP Flux Determinations

Flux of SRP across the sediment–water interface was determined by monitoring the change in SRP concentration in overlying water through time. July and September experiments ran for 19 d and October experiments for 49 d. SRP flux was calculated as milligrams PO_4-P per square metre per day.

Macroinvertebrate Enumeration

Following incubation, cores were preserved in 10% buffered formalin. Animals were later separated with a sugar solution

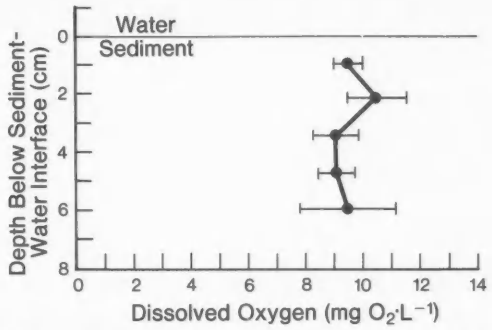

FIG. 3. Mean dissolved oxygen concentration (±SE, n = 3) in pore water versus depth below the sediment–water interface.

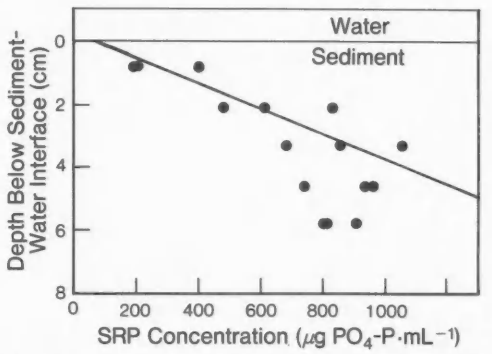

FIG. 4. SRP pore water concentration (±SE, n = 3) versus depth below the sediment–water interface. Linear least squares fit of data is shown.

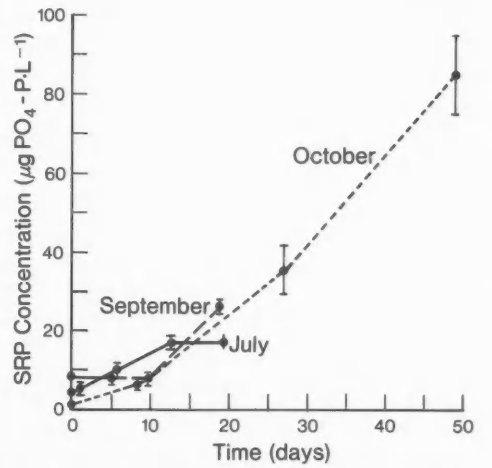

FIG. 5. Mean SRP concentration (±SE) in overlying water of test cores versus time for July, September, and October experiments.

floatation/sieving technique (250-μm pore size; Nalepa and Quigley 1980). Major macroinvertebrate groups, (oligochaetes, chironomids, amphipods, and pisidiid clams) were separated and counted in a white enamel pan without magnification. Biomass of resident oligochaete worm communities

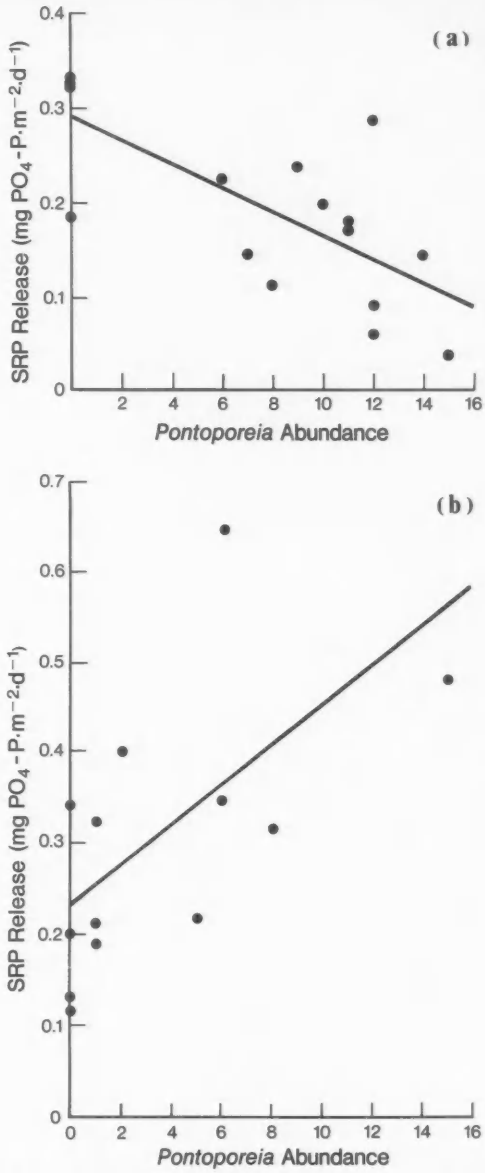

FIG. 6. *Pontoporeia* abundance versus SRP release rate in individual test cores of the (a) July experiment and (b) October experiment. Regression analysis produced lines (shown) with slopes of −0.46 in July and 0.76 in October with respective intercepts of 10.64 and 8.23.

was determined by extrapolating overall length to weight (Nalepa and Quigley 1980, 1983).

Results

Dissolved Oxygen and SRP Concentration in Pore Waters

Dissolved oxygen concentrations in pore waters remained high throughout the upper 6 cm sediment layer (Fig. 3). By contrast, SRP concentrations (Fig. 4) were low near the sediment–water interface increasing with depth to 3 cm. From

TABLE 1. Published SRP pore water concentrations for a variety of lake and river sediments.

Location	SRP pore water concentration ($\mu g\ PO_4\text{-}P \cdot mL^{-1}$)	Reference
Eutrophic Lakes (western U.S.)	0.08–10.5	Gahler 1968
White Lake, eutrophic (Michigan)	2.5–3.5 (upper 5 cm sediment)	Freedman and Canale 1977
Lake Mendota, eutrophic (Wisconsin)	2.0	Holdren 1976
Castle Lake, mesotrophic (California)	0.2	Neame 1977
Lake Constance, eutrophic (Germany)	0.06–0.15	Wagner 1968
Lake Ontario, nearshore	0.02–0.59	Bannerman et al. 1974
Potomac River	Up to 1.55	Callender and Hammond 1982
Lake Michigan, nearshore (upper 5 cm)	0.27–0.88	Present study

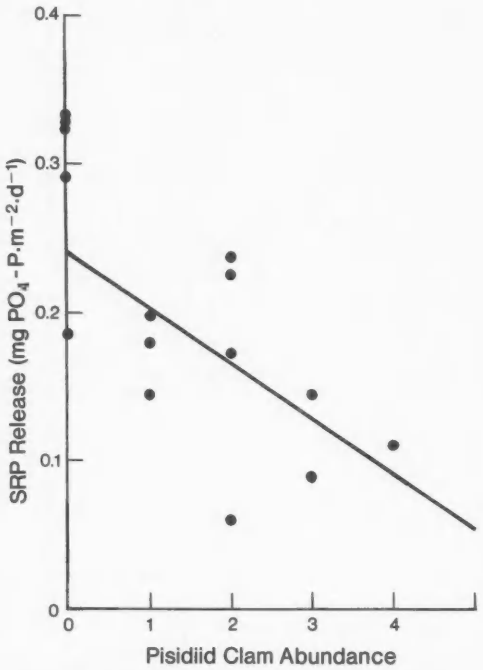

FIG. 7. Pisidiid clam abundance versus SRP release rate in individual test cores of the July experiment. Regression analysis produced a line (shown) with a slope of −1.38 and an intercept of 8.79.

3 to 6 cm, SRP concentration remained constant.

SRP Flux Based on Pore Water Concentration Gradients

We used a Fickian diffusive flux equation (Fick 1855) to estimate SRP release from sediments based on the SRP pore water gradient and physical sediment properties where

$$(1)\quad J_s = -\phi \frac{D}{\theta^2} \frac{\partial C}{\partial x}\bigg|_{x=0} A$$

where J_s = the SRP flux across the sediment–water interface (milligrams PO_4-P per square metre per day), $\phi = 0.50$, the porosity (percent water by volume) of the uppermost 1 cm sediment layer, $D = 381.41 \cdot cm^{-2} \cdot yr^{-1}$, the diffusion coefficient of PO_4 in free freshwater solution with a temperature correction (12°C) (Robbins 1980; Li and Gregory 1974), θ = a tortuosity term that depends on the size, shape, and packing of sediment particles, although its relation to porosity is not well-understood (Berner 1980): $\theta^2 = \phi F$ where $F = \phi^{-n}$ (for sands, Archie (1942) empirically determined an n of 1.3 and thus θ is equal to 1.11), $\partial C/\partial x|_{x=0}$ = the SRP concentration gradient at the sediment–water interface, which was calculated from measured SRP pore water concentrations (we relied on linear regressions of four data points from each of three peepers (where sediment depth <3.3 cm); the mean gradient, calculated from slopes of the three lines, was 0.263 ± 0.032 (SE) $\mu g\ PO_4\text{-}P \cdot cm^{-4}$), and A = a proportionality constant of 27.397 $\times 10^{-3}$ used in converting from flux units of micrograms PO_4-P per square centimetre per year to more common units of milligrams PO_4-P per square metre per day. Multiplication of terms in equation 1 produced an estimated diffusive flux of 1.12 mg $PO_4\text{-}P \cdot m^{-2} \cdot d^{-1}$ ± 0.14 (SE).

SRP Release from Sediment Cores

In general, SRP concentration in overlying water of cores increased with time (Fig. 5), although September cores showed little SRP release within the first 10 d of incubation and July cores showed little SRP release over days 12–18.

Calculated mean SRP release rates (± SE) were 0.19 ± 0.03, 0.17 ± 0.03, and 0.57 ± 0.04 mg $PO_4\text{-}P \cdot m^{-2} \cdot d^{-1}$ on July, September, and October sampling dates, respectively. These rates were derived from net changes in SRP concentrations in overlying water during the entire incubation period within each of the three experiments. As a result, July and September determinations are generally conservative estimates because they are based on overall change in SRP rather than the more rapid changes found between certain sampling intervals.

Macroinvertebrate Abundance and SRP Release Rate in Individual Cores

Overall, linear correlation coefficients calculated between SRP flux and abundance of the amphipod *Pontoporeia hoyi*, chironomids, and oligochaetes were not significant ($P < 0.05$). However, significant correlation did exist between *P. hoyi* abundance and SRP flux in July ($r = -0.70$) and October ($r = 0.61$) (Fig. 6a and 6b). We also noted a significant r

TABLE 2. Published SRP flux estimates from aerobic lake and

Lake	Status	Temp. (°C)	D
Lake Mendota (Wisconsin)	Eutrophic	—	
Lake Mendota (Wisconsin)	Eutrophic	20	
Lake Mendota (Wisconsin)	Eutrophic	2–23	5
Wingra (Wisconsin)	Eutrophic	4–21	
Minocqua (Wisconsin)	Mesotrophic	3–18	5
Little John (Wisconsin)	Eutrophic	4–16	5
Lake Esrom (Denmark)	Eutrophic	20	
Lake Esrom (Denmark)	Eutrophic	7	
Fureso (Denmark)	Eutrophic	7	
Grane Langso (Denmark)	Oligotrophic	7	
St. Gribso (Denmark)	Dystrophic	7	
Castle Lake (California)	Mesotrophic	—	
Lake Warner (Massachusetts)	Eutrophic	24–30	
Lake Constance (Germany)	Eutrophic	15	
Lake Erie (Central Basin)	Eutrophic	—	
Lake Ontario (inshore silts)	Mesotrophic	—	
Lake Ontario (inshore silts)	Mesotrophic	—	
Lake Michigan (SE nearshore)	Mesotrophic	12	
Lake Michigan (SE nearshore)	Mesotrophic		

[a]95% confidence interval.

ake and river sediments.

p.)	Depth (m)	Method of determination	SRP flux (mg PO_4-P·m^{-2}·d^{-1})	Reference
-	—	Core incubation	1.00−5.00	Holdren 1976
)	—	Core incubation	0.00−9.00	Gallepp 1979
23	5−6	Core incubation	(−1.92)−83.01	Holdren and Armstrong 1980
21	3.5	Core incubation	(−0.60)−3.40	Holdren and Armstrong 1980
18	5−6	Core incubation	0.02−0.41	Holdren and Armstrong 1980
16	5−6	Core incubation	0.02−1.10	Holdren and Armstrong 1980
)	3	Core incubation	(−8.00)−16.11	Kamp-Nielsen 1975
7	22	Core incubation	−1.40±0.70[a]	Kamp-Nielsen 1974
7	36	Core incubation	−2.00±1.80[a]	Kamp-Nielsen 1974
7	11.5	Core incubation	0.60±0.10[a]	Kamp-Nielsen 1974
7	11	Core incubation	0.20±0.20[a]	Kamp-Nielsen 1974
-	4	^{32}P tracer		
30	—	Homogenized sediment incubation	0.65	Neame 1977
5	—	Homogenized sediment incubation	1.20	Fillos and Swanson 1975
-	—	Mass balance calculation based on O_2 depletion/ CO_2 increase	3.51	Banoub 1975
-	—	Core incubation	0.68	Burns and Ross 1972
-	—	Predicted from pore water gradient	0.80	Bannerman et al. 1974
			0.05−0.60	Bannerman et al. 1974
2	11	Core incubation	0.17−0.57	Present study
		Predicted from pore water gradient	1.12±0.14 (SE)	Present study

(−0.52) between SRP flux and pisidiid clam abundance in July experiments (Fig. 7).

Discussion

Dissolved Oxygen and SRP Concentrations in Pore Water

Pore water profiles of dissolved oxygen concentration (Fig. 3) show nearshore sediments to be well-oxygenated to a depth of at least 6 cm. These results agree closely with previous observations (Marzolf 1962; Nalepa and Robertson 1981). The presence of oxygen at near-saturation levels has also been noted for comparable depth intervals of sand substrates in rivers (Poole and Stewart 1976; Whitman and Clark 1982).

Despite high dissolved oxygen concentration in the upper 6 cm sediment layer, SRP concentration increased rapidly with depth through the upper half of this zone. This trend is surprising given that phosphorus commonly coprecipitates with Fe, Mn, or Al in oxide−hydroxide complexes (Syers et al. 1973). Although additional phosphorus may be temporarily immobilized by microbial activity (Doremus and Clesceri 1982) or through sorption to sediment particles (Li et al. 1972), nearshore Lake Michigan pore water contains unexpectedly high SRP concentrations. These levels may be related to the coarseness (270-μm median particle size) of our nearshore sediments. Eadie et al. (1984) noted that among particles collected in near-bottom sediment traps in southeastern Lake Michigan, there was very little phosphorus associated with particles larger than 64 μm, while finer particles were chemically enriched. This difference may result from the fact that clays may have up to 90 times more surface area (on a weight basis) than sands (Weiler and Mills 1965). With relatively low surface area, nearshore sands provide fewer available sites for phosphorus sorption and less overall area for microbial colonization (and associated phosphorus uptake). As a result, sands may have a low overall sorptive capacity for phosphorus. When this capacity is exceeded, SRP can be expected to accumulate in pore water.

In general, Lake Michigan nearshore SRP pore water concentrations were lower than those noted for two eutrophic lakes and most similar to those found in nearshore Lake Ontario (Table 1).

Measured SRP from Cores

Previous aerobic SRP flux measurements from sediment cores and fluxes predicted from pore water SRP gradients are wide-ranging and include both negative fluxes (SRP flux into sediments) and positive fluxes (SRP out of sediments) (Table 2). Core experiments frequently had minimal replication and wide variation about means.

The range of SRP (0.17−0.57 mg PO_4-P·m^{-2}·d^{-1}) we noted for nearshore Lake Michigan sediments was below the 0.80 mg PO_4-P·m^{-2}·d^{-1} value found for inshore Lake Ontario silts (Bannerman et al. 1974). Our flux values (Table 2) were closest to rates of an oligotrophic Danish lake (Grane Langso, 0.60 mg PO_4-P·m^{-2}·d^{-1}), a dystrophic Danish lake (St. Gribso, 0.20 mg PO_4-P·m^{-2}·d^{-1}), and an estimate of 0.65 mg PO_4-P for a mesotrophic California lake (Castle Lake) that was derived from core radiotracer studies.

The SRP flux from sediments predicted by a Fickian diffusive flux equation (1.12 ± 0.14 (SE) mg PO_4-P·m^{-2}·d^{-1}) was 2−7 times larger than actual fluxes measured from cores. The difference between actual and predicted fluxes may arise from the inability to account realistically for phosphorus sorption within our Fickian diffusive flux equation. Undoubtedly a substantial amount of SRP may sorb to sediments during upward diffusion, with the greatest potential for phosphorus sorption occurring in the uppermost sediments where fine particles are most abundant. Our predicted flux was also larger than the range of fluxes estimated from Lake Ontario pore water data (Table 2).

In summary, despite high dissolved oxygen levels in pore waters, SRP concentrations remain relatively high; this indicates that most or all of the actual SRP release we measured from cores is probably derived from diffusion out of pore water into overlying water.

Macroinvertebrate Abundance and SRP Release from Individual Cores

We found only a few instances of significant ($P < 0.05$) correlation between SRP flux from individual cores and corresponding abundance or biomass of resident macroinvertebrates. However, significant correlations did exist for *P. hoyi* abundance during July (Fig. 6a) and October (Fig. 6b), suggesting that activities of the amphipod may affect SRP exchange across the sediment−water interface. Moreover, a significant r between SRP flux and pisidiid clam abundance in individual cores during July implies that this macroinvertebrate group may also influence SRP release from nearshore Lake Michigan sediments. *Pontoporeia hoyi* are known to: (1) reduce the release of soluble reactive silica from nearshore Lake Michigan sediments with increasing abundance in intact cores (Quigley and Robbins 1984), (2) mix surficial Great Lakes sediments in an eddy-diffusive manner during feeding and burrowing (Robbins et al. 1979), and (3) enhance solute diffusion from sediments by 70% through burrowing activity (Krezoski et al. 1984). In addition, deposit-feeding by pisidiid clams (Monakov 1972) may affect SRP release in ways similar to *P. hoyi*.

In light of the above evidence, and that of our study, the role of macroinvertebrates in affecting SRP exchange at the sediment−water interface warrants further examination.

SRP Regeneration and Nearshore Nutrient Dynamics

Our results demonstrate that nearshore sediments constitute a source of SRP to overlying water despite the presence of a thick well-oxygenated sediment layer. Water quality in Lake Michigan's nearshore zone, where phosphorus loading is disproportionately large because of tributary inputs, differs greatly from offshore waters. The nearshore zone contains greater standing crops of nearshore phytoplankton that, in part, result from higher nutrient loading (Schelske 1980). This difference has also been attributed to additional physical, chemical, and biological characteristics of the nearshore area that are not well-understood (Beeton and Edmondson 1972).

To our knowledge, the aerobic release of phosphorus from nearshore Lake Michigan sediments has not been previously reported, and we contend that this process merits inclusion in future conceptual models of Lake Michigan's phosphorus cycle.

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References

AMERICAN PUBLIC HEALTH ASSOCIATION, AMERICAN WATER WORKS ASSOCIATION, AND WATER POLLUTION CONTROL FEDERATION. 1976. Standard methods for the examination of water and wastewater, including bottom sediment and sludges. 14th ed. Washington, DC. 1193 p.

ARCHIE, G. E. 1942. The electrical resistivity log as an aid in determining some reservoir characteristics. Am. Inst. Mech. Eng. Trans. 146: 54–61.

BANNERMAN, R. T., D. E. ARMSTRONG, G. C. HOLDREN, AND R. F. HARRIS. 1974. Phosphorus mobility in Lake Ontario sediments, p. 158–178, *In* Proceedings of the 17th Conference on Great Lakes Research, Ann Arbor, MI.

BANOUB, M. W. 1975. Experimental studies on material transactions between mud and water of the Gnadensee (Bodensee). Verh. Int. Ver. Limnol. 19: 1263–1271.

BEETON, A. M., AND W. T. EDMONDSON. 1972. The eutrophication problem. J. Fish. Res. Board Can. 29: 673–682.

BERNER, R. A. 1980. Early diagenesis: a theoretical approach. Princeton University Press, Princeton, NJ. 241 p.

BURNS, N. M., AND C. ROSS. 1972. Project HYPO: an intensive study of the Lake Erie Central Basin hypolimnion and related surface water phenomena. U.S. EPA Tech. Rep. TS-05-71-208-24, Canada Center for Inland Waters, Burlington, Ont., and Environmental Protection Agency, Ohio District Basin Office, Fairview Park, OH. 182 p + XII.

CALLENDER, E., AND D. E. HAMMOND. 1982. Nutrient exchange across the sediment–water interface in the Potomac River estuary. Estuarine Coastal Shelf Sci. 15: 395–414.

CHAMBERS, R. L., AND B. J. EADIE. 1980. Nearshore chemistry in the vicinity of the Grand River, Michigan. NOAA Tech. Memo. ERL GLERL-28, National Technical Information Service, Springfield, VA 22161. 33 p.

DILLON, P. J., AND F. G. RIGLER. 1974. A test of a simple nutrient budget model predicting the phosphorus concentration in lake water. J. Fish. Res. Board Can. 32: 1519–1531.

DOREMUS, C., AND L. S. CLESCERI. 1982. Microbial metabolism in surface sediments and its role in the immobilization of phosphorus in oligotrophic lake sediments. Hydrobiologia 91: 261–268.

EADIE, B. J., R. L. CHAMBERS, W. S. GARDNER, AND G. L. BELL. 1984. Sediment trap studies in Lake Michigan: resuspension and chemical fluxes in the southern basin. J. Great Lakes Res. 10: 307–321.

EADIE, B. J., R. L. CHAMBERS, J. M. MALCZYK, AND A. LANGSTON. 1979. The effect of the Grand River spring runoff on Lake Michigan. Pollution from Land Use Activities Group Task D, Subactivity 3–1, Special International Joint Commission PLUARG Report, International Joint Commission, Windsor, Ont. 91 p.

FICK, A. 1855. Ueber Diffusion. Ann. Phys. (Leipzig) 170: 59–86.

FILLOS, J., AND W. R. SWANSON. 1975. The release rate of nutrients from river and lake sediments. J. Water Pollut. Control Fed. 47: 1032–1042.

FOX, H. M., AND C. A. WINGFIELD. 1938. A portable apparatus for the determination of oxygen dissolved in a small volume of water. J. Exp. Biol. 15: 437–445.

FREEDMAN , P. L., AND R. P. CANALE. 1977. Nutrient release from anaerobic sediments. J. Env. Eng. Div., ASCE 103: 233–244.

GAHLER, A. R. 1969. Sediment–water nutrient interchange, p. 243–257. *In* Proceedings of the Eutrophication–Biostimulation Workshop, University of California, Berkeley, CA.

GALLEPP, G. W. 1979. Chironomid influence and phosphorus release in sediment–water microcosms. Ecology 60: 547–556.

GARDNER, W. S., T. F. NALEPA, M. A. QUIGLEY, AND J. M. MALCZYK. 1981. Release of phosphorus by certain benthic invertebrates. Can. J. Fish. Aquat. Sci. 38: 978–981.

GRANELI, W. 1979. The influence of *Chironomus plumosus* on the exchange of dissolved substances between sediment and water. Hydrobiologia 66: 149–159.

HESSLEIN, R. H. 1976. An in situ sampler for close interval pore water studies. Limnol. Oceanogr. 21: 912–914.

HOLDREN, G. C. 1976. Measurement of interstitial inorganic phosphorus and phosphorus release from lake sediment. M.S. thesis, University of Wisconsin, Madison, WI. 171 p.

HOLDREN, G. C., AND D. E. ARMSTRONG. 1980. Factors affecting phosphorus release from intact lake sediment cores. Environ. Sci. Technol. 14: 79–87.

KAMP-NIELSEN, L. 1974. Mud–water exchange of phosphate and other ions in undisturbed sediment cores and factors affecting the exchange rates. Arch. Hydrobiol. 73: 218–237.

1975. Seasonal variation in sediment–water exchange of nutrient ions in Lake Esrom. Verh. Int. Ver. Limnol. 19: 1057–1065.

KREZOSKI, J. R., J. A. ROBBINS, AND D. S. WHITE. 1984. Dual radiotracer measurement of zoobenthos-mediated solute and particle transport in freshwater sediments. J. Geophys. Res. 89: 7937–7947.

LEE, G. F. 1970. Factors affecting the transfer of materials between water and sediments. Lit. Rev. No. 1, Water Resources Center, University of Wisconsin, Madison, WI. 50 p.

LEE, G. F., W. C. SONZOGNI, AND R. D. SPEAR. 1977. Significance of oxic versus anoxic conditions for Lake Mendota sediment phosphorus release, p. 259–308. *In* Phosphorus management strategies for lakes. Ann Arbor Science Publishers Inc., Ann Arbor, MI.

LI, W. C., D. E. ARMSTRONG, J. D. WILLIAMS, R. F. HARRIS, AND J. K. SYERS. 1972. Rate and extent of inorganic phosphate exchange in lake sediments. Proc. Soil Sci. Soc. Am. 36: 279–285.

LI, Y. H., AND S. GREGORY. 1974. Diffusion of ions in sea water and in deep sea sediments. Geochim. Cosmochim. Acta 38: 703–714.

MARZOLF, G. R. 1962. Substrate relations of the burrowing amphipod *Pontoporeia affinis* Lindstrom. Ph.D. dissertation, University of Michigan, Ann Arbor, MI. 92 + VII p.

MONAKOV, A. V. 1972. Review of studies on feeding of aquatic invertebrates conducted at the Institute of Biology of Inland Waters, Academy of Sciences, USSR. J. Fish. Res. Board Can. 29: 363–383.

MORTIMER, C. H. 1941. The exchange of dissolved substances between mud and water in lakes. J. Ecol. 29: 280–329.

1942. The exchange of dissolved substances between mud and water in lakes, Part III — Summary and Part — IV References. J. Ecol. 30: 147–201.

1971. Chemical exchanges between sediment and water in the Great Lakes: speculations on probable regulatory mechanisms. Limnol. Oceanogr. 16: 387–404.

1975. Environmental status of the Lake Michigan region. Vol. 2. Physical limnology of Lake Michigan. Part 1. Physical characteristics of Lake Michigan and its response to applied forces. Argonne National Laboratory, Argonne, IL, ANL/ES-40 Vol. 2: 13–102.

NALEPA, T. F., AND M. A. QUIGLEY. 1980. The macro- and meiobenthos of southeastern Lake Michigan near the mouth of the Grand River, 1976–1977. NOAA Data Rep. ERL GLERL-17, National Technical Information Service, Springfield, VA 22161. 16 p. + microfiche.

1983. Abundance and biomass of the meiobenthos in nearshore Lake Michigan with comparisons to the macrobenthos. J. Great Lakes Res. 9: 530–547.

NALEPA, T. F., AND A. ROBERTSON. 1981. Vertical distribution of the zoobenthos of southeastern Lake Michigan with evidence of seasonal variation. Freshwater Biol. 11: 87–96.

NEAME, P. A. 1977. Phosphorus flux across the sediment–water interface, p. 307–312. *In* H. L. Golterman [ed.] Interactions between sediments and freshwaters. D. V. Junk bv Publishers, The Hague, The Netherlands.

POOLE, W. C., AND K. W. STEWART. 1976. The vertical distribution of macrobenthos within the substratum of the Brazos River, Texas. Hydrobiologia 50: 151–160.

QUIGLEY, M. A., AND J. A. ROBBINS. 1984. Silica regeneration processes in nearshore southern Lake Michigan. J. Great Lakes Res. 10: 388–392.

ROBBINS, J. A. 1980. Sediments of southern Lake Huron: elemental composition and accumulation rates. U.S. EPA Rep. No. EPA-600/3-80-080, Environmental Research Laboratory, Duluth, MN. 310 + xx p.

ROBBINS, J. A., P. L. MCCALL, J. B. FISHER, AND J. R. KREZOSKI. 1979. Effects of deposit-feeding on migration of ^{137}Cs in lake sediments. Earth Planet. Sci. Lett. 42: 277–287.

SCHELSKE, C. L. 1980. Dynamics of nutrient enrichment in large lakes: the Lake Michigan case, p. 42–46. *In* Restoration of Lakes and Inland Waters: Proceedings of the International Symposium on Inland Waters and Lake Restoration. U.S. EPA Rep. No. EPA-440/5-81-010, U.S. EPA Office of Regulations and Standards, Washington, DC.

SYERS, J. K., R. F. HARRIS, AND D. E. ARMSTRONG. 1973. Phosphate chemistry in lake sediments. J. Environ. Qual. 2: 1–14.

WAGNER, G. 1968. Lake Constance sediments. Petrographical, mineralogical, and chemical studies on sediments in the delta region of the Schussen and Argen rivers. Schweiz. Z. Hydrol. 30: 75.

WEILER, R. R., AND A. A. MILLS. 1965. Surface properties and pore structure of marine sediments. Deep-Sea Res. 12: 511–552.

WHITMAN, R. L., AND W. J. CLARK. 1982. Availability of dissolved oxygen in interstitial waters of a sandy creek. Hydrobiologia 92: 651–658.

Delayed Metamorphosis with Reduced Larval Growth in a Coral Reef Fish (*Thalassoma bifasciatum*)

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Victor, B. C. 1986. Delayed metamorphosis with reduced larval growth in a coral reef fish (*Thalassoma bifasciatum*). Can. J. Fish. Aquat. Sci. 43: 1208–1213.

Analyses of daily otolith increment sequences in the bluehead wrasse, *Thalassoma bifasciatum*, from the San Blas Islands of Panama indicated that (1) the duration of the planktonic larval period of this species ranges from 38 to 78 d, (2) those larvae with extended larval durations reach settlement size at the same age as average individuals but then remain planktonic for several more weeks, and (3) the estimated larval growth rate during this period of delayed metamorphosis (0.08 $mm \cdot d^{-1}$) is distinctly lower than both the estimated growth rate before attaining settlement size (0.26 $mm \cdot d^{-1}$) as well as the growth rate of juveniles after settlement (0.31 $mm \cdot d^{-1}$). The ability to delay metamorphosis, the first documented for a vertebrate, may be an adaptation for maximizing the return of planktonic larvae to coastal waters.

L'analyse de séries de croissance quotidiennes des otolithes chez le labre *Thalassoma bifasciatum* des îles San Blas de Panama a montré que : (1) la durée de la période larvaire planctonique variait de 38 à 78 jours chez cette espèce, (2) les larves à stade larvaire plus long atteignaient la taille de retour aux coraux au même âge que les individus à période larvaire moyenne, mais qu'ils continuaient d'être planctoniques pendant plusieurs autres semaines et (3) le taux estimé de croissance larvaire au cours de cette période de retard de la métamorphose (0,08 $mm \cdot jour^{-1}$) était distinctement inférieur au taux de croissance estimé avant le moment où la taille de retour était atteinte (0,26 $mm \cdot jour^{-1}$) ainsi qu'au taux de croissance des juvéniles après le retour (0,31 $mm \cdot jour^{-1}$). Cette capacité de retarder la métamorphose, la première à être décrite chez un vertébré, peut s'expliquer par une adaptation visant à maximiser le retour des larves planctoniques vers les eaux côtières.

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Larval settlement and metamorphosis in a number of invertebrate phyla do not have to occur at a fixed age but can be delayed, especially in the absence of suitable settlement cues (see review in Jackson and Strathmann 1981). The period of delay can last for weeks in many cases, and for months in various gastropods (Scheltema 1971; Pechenik et al. 1984), enteropneusts (Hadfield 1978), asteroids (Domanski 1984), and corals (Richmond 1985). Some of these species are able to disperse over great distances, presumably as a result of this flexibility in their timing of settlement and metamorphosis (Scheltema 1971; Scheltema and Williams 1983; Pechenik et al. 1984; Richmond 1985). Some widely dispersing, or teleplanic, larvae apparently experience a marked reduction in their growth rate after becoming competent to settle, perhaps because a larger size in the plankton would reduce survival (Scheltema 1971; Pechenik et al. 1984).

Although the delay of larval settlement and metamorphosis is apparently widespread among invertebrates, it has not yet been documented in a vertebrate, despite the fact that virtually all tropical marine fishes and most temperate marine fishes have planktonic larvae (Breder and Rosen 1966; Sale 1980). This is most likely a result of the general lack of information on the early life history of marine fishes, and, furthermore, the difficulties in manipulating captive larvae of nonpelagic species (laboratory studies of marine fish larvae have typically been performed on pelagic species, see Lasker 1981).

As a result of the recent development of the daily otolith increment aging technique, it is now possible to examine aspects of the planktonic life and the timing of settlement of fish larvae under natural conditions. The presence of distinct daily incremental marks on the otoliths of bony fishes permits one to age individual fishes with remarkable precision as well as to estimate the increment of growth for each day of their life (Panella 1980; review in Campana and Neilson 1985). In addition, both daily increments and a conspicuous mark corresponding to settlement of the planktonic larva have been experimentally verified to be on the otoliths of some coral reef wrasses (Victor 1982, 1983). In this study, I use this new technique to ascertain first whether larvae of the Caribbean bluehead wrasse, *Thalassoma bifasciatum*, are capable of delaying settlement after becoming competent to settle (defined here as attaining settlement size), and second, whether these fish larvae also exhibit reduced growth rates during the period of delay.

Materials and Methods

I collected 1125 bluehead wrasses, mostly juveniles, from various patch reefs at the western end of the San Blas Archipelago on the Caribbean coast of Panama between 1981 and

1983. In addition to this broad sample, I captured 47 newly settled bluehead wrasses from Ukubtupo Reef in the San Blas Islands. To ensure that these new recruits were caught on the first day of their appearance on the reef, I censused the bluehead wrasse population on a number of coral outcrops in a seagrass bed each day over an 18-mo period in 1981 and 1982. Recruits of this species avoid sand and seagrass and prefer to settle onto coral outcrops, where they tend to remain for at least several weeks (Victor 1986a). I collected new recruits only when they first appeared on an outcrop that was isolated from other outcrops and had not had a bluehead wrasse resident for weeks prior to the new recruit's arrival.

The fish were captured by hand with an aquarium dipnet and immediately preserved in 95% ethanol. They were later measured to the nearest 0.1 mm standard length (SL) and two of the three pairs of otoliths were extracted from each individual. The larger pair, the sagittae, were removed with fine forceps from their pockets at the base of the cranium, while the midsized pair, the lapilli, were removed from the lateral walls of the brain case. The otoliths were subsequently cleaned and dried and placed in a drop of immersion oil on a glass microscope slide.

I examined the otoliths under a compound microscope with transmitted light at magnifications of from 400 to 1000×. Daily increments are clearly visible on the otoliths of both larval and juvenile wrasses without any special preparation. The increments are more distinct if the otoliths have remained in immersion oil for at least several weeks and if a polarizing filter is placed between the light source and the slide. I calculated the planktonic larval duration for each of the fish by counting the number of daily increments between the center of the otolith and the settlement mark and adding 2 d, the estimated time between fertilization and the first formation of the otoliths (Victor 1982). The growth rate of recently settled juveniles was derived from the relationship between the age since settlement and fish length (individuals <50 d postsettlement, $n = 694$). I estimated the age since settlement by counting the number of daily increments between the settlement mark and the edge of the otolith (Victor 1982).

The width of each increment from within the larval period was recorded for 10 fish with the modal larval duration (47 d) and 15 fish with extended larval durations (>62 d), drawn from the entire sample of bluehead wrasses from Panama. I measured increment widths to the nearest 0.1 μm along the longest radius of one of the sagittae (center to posterior tip) with the aid of a computerized digitizing board overlay on a videoscreen image of the otolith at a microscope magnification of 1000×.

The daily growth rate of bluehead wrasse larvae was estimated by back-calculating larval lengths from observed otolith radii. The mean otolith radius for each day of the larval life was derived by summing the sequence of mean daily increment widths leading up to that day (means of the 25 individuals whose otolith increment widths were recorded). Assuming that bluehead wrasses have a linear relationship between fish length and sagitta radius, one can predict the length of a larva at any previous age from the corresponding otolith radius if the equation for this line were known. Bluehead wrasse larvae hatch at 1.1 mm SL, at about the time their otoliths first appear (pers. obs.). Furthermore, new recruits with a larval duration of 42 d had a mean SL of 11.0 mm (this study) and a mean sagitta radius of 135.6 μm up to the settlement mark at the edge of their otoliths. The relationship between fish standard length and sagitta radius is therefore

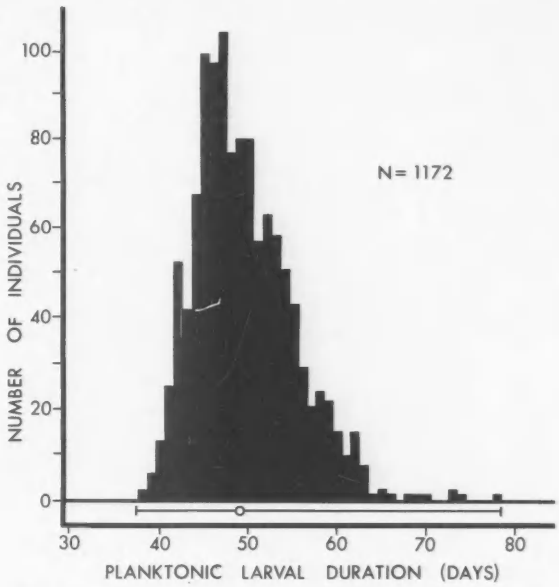

FIG. 1. Distribution of durations of the planktonic larval phase of bluehead wrasses from the San Blas Islands of Panama. Mean and range are represented below the horizontal axis. The sample includes 1125 juveniles and adults from San Blas patch reefs and 47 newly settled individuals from Ukubtupo Reef.

$$\text{Standard length (mm)} = 0.073\,(\text{sagitta radius } (\mu\text{m})) + 1.1.$$

This equation was used to estimate standard lengths for the mean sagitta radii corresponding to each day in the life of bluehead wrasse larvae.

Results

The larval durations of bluehead wrasses from the San Blas Islands ranged from 38 to 78 d, with a mean of 49.3 d and a mode at 47 d (SD = 5.5 d). The distribution was skewed, with a number of individuals having distinctly longer larval durations (Fig. 1). The widths of the daily increments steadily increased during the larval period until the beginning of the seventh week of larval life, at which point the daily increments narrowed abruptly (Fig. 2). This transition occurred in larvae with average larval durations as well as in those that had extended larval durations (Fig. 3). The mean width of the increments after the seventh week, 1.7 μm, was significantly narrower than the mean width for the first 6 wk, 3.4 μm (calculated from those individuals with larval lives longer than 62 d, paired t-tests, $n = 15$, $p < 0.0001$). Furthermore, the mean increment width for the first 47 d of larval life of those individuals with an extended larval duration was not significantly different from the mean width for that same period of fish with average larval durations (means of 3.3 and 3.4 μm, SD = 0.5 and 0.6 μm, $n = 15$ and 10, respectively; t-test $p > 0.63$).

Since the widths of the daily increments corresponding to the first 47 d for fish with extended larval durations were no different from those of fish with average larval durations, one can infer that within an age class (at least up to day 47), larvae that were destined to remain in the plankton longer were similar

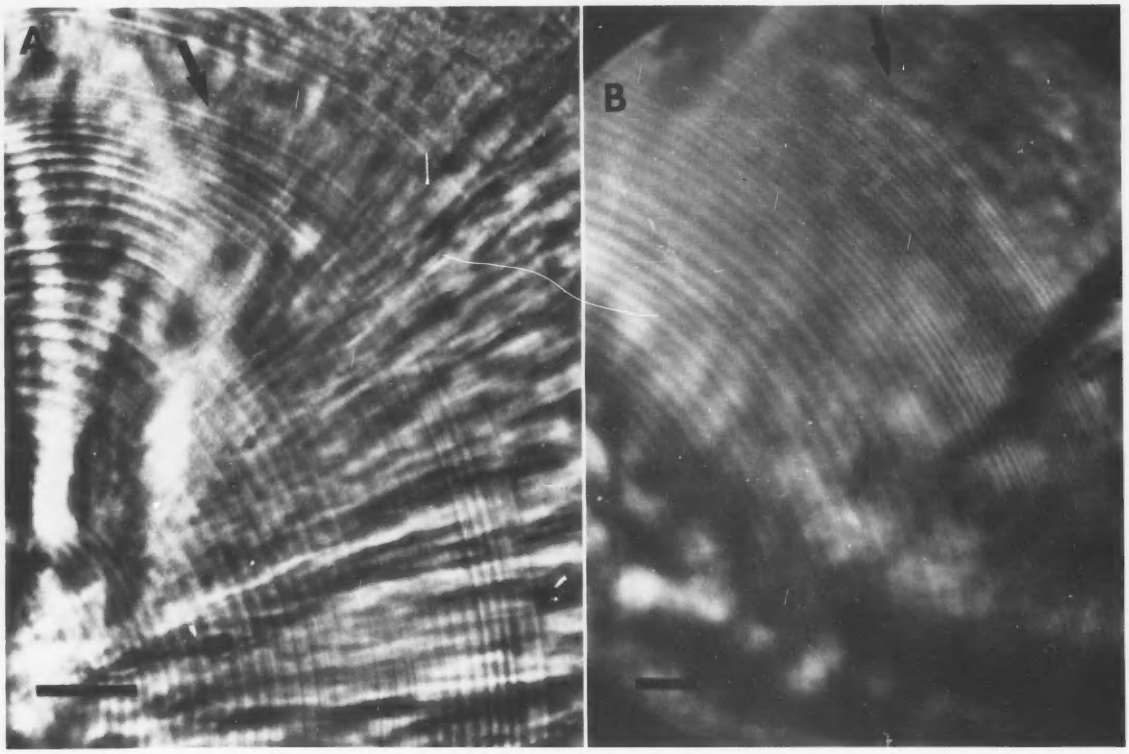

FIG. 2. (A) Sagitta of a 14.3 mm SL bluehead wrasse with the modal larval duration; (B) sagitta of a 16.1 mm SL bluehead wrasse with an extended larval duration of 63 d. Bars = 25 μm. The arrows indicate the settlement transition. The centers of the sagittae are out of the frame to the lower left.

in size to those that were settling. Given that both kinds of larvae attained a competent size at the same age, the observed change in size at settlement with increasing larval duration would therefore be one estimate of the rate of growth during the period of delay. The size of newly settled bluehead wrasses on Ukubtupo Reef ranged from 10.4 to 13.0 mm SL ($\bar{x}$ = 11.6 mm, SD = 0.7 mm, n = 47). There was a significant increase in the size of new recruits with increased larval duration, indicating a growth rate of 0.08 mm·d^{-1} during the delay period ($y = 0.083x + 7.522$, $p < 0.0001$, $r^2 = 0.52$; Fig. 4B, solid line).

Back-calculations of fish length corresponding to previous otolith radii can provide a second, and independent, estimate of daily growth rates in the plankton. Indeed, this method is the only way of estimating daily larval growth rates before competency, since wild-caught larvae were not available for this study (a crude estimate of the overall precompetent larval growth rate can also be derived simply by dividing the change in size over the precompetent larval period, 11.0−1.1 mm, by the length of the period, 42 d, yielding 0.24 mm·d^{-1}). On the other hand, larval growth rates during the period of delay after competency can be estimated both by the back-calculation method as well as by the change in size of new recruits with increased larval duration described above (Fig. 4B). Back-calculations indicated that the growth rate of bluehead wrasse larvae after hatching started out at about 0.18 mm·d^{-1} and reached 0.26 mm·d^{-1} as they approached settlement size (Fig. 4A). Back-calculations also indicated that the growth rate of larvae during the delay period was 0.13 mm·d^{-1} (Fig. 4B, broken line). The growth rate of juvenile bluehead wrasses for the first 50 d after settlement (estimated by the change in size with age since settlement) was 0.31 mm·d^{-1}, distinctly higher than the estimated rates of larval growth (Fig. 4C). The larval duration did not affect subsequent growth rates on the reef; individuals with larval durations more than one standard deviation from the mean (55 d or longer and 43 d or shorter) grew at an identical rate to fish within one standard deviation from the mean (0.31 mm·d^{-1} for all three groups, total n = 694).

Discussion

The relative ease with which invertebrate larvae can be maintained and manipulated in captivity has resulted in a large body of research detailing the duration of larval development, the feeding and growth of larvae, and the cues for metamorphosis and settlement of a wide variety of marine invertebrates (e.g. Chia and Rice 1978). In comparison, information on the ecology of marine fish larvae is scarce. The recent development of the daily increment aging technique, however, should permit access to even more precise and valuable information than is obtainable by the methods currently employed by invertebrate zoologists. The otolith can contain a daily record of the growth and, in some cases, even subtle changes in the life history of individual fish in the field. It is the acquisition of information

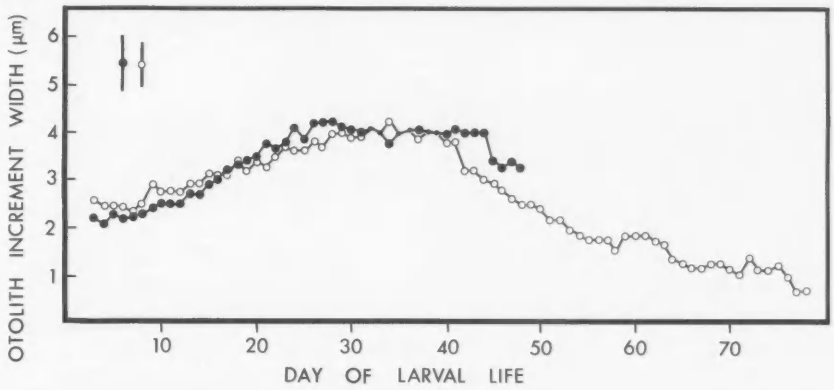

FIG. 3. Mean increment width along the longest radius of the sagitta for each day of the larval life of bluehead wrasses with modal larval durations (solid circles, $n = 10$) and with extended larval durations (open circles, $n = 15$). The average 95% confidence intervals of the means of both samples for the first 48 d are indicated at the upper left.

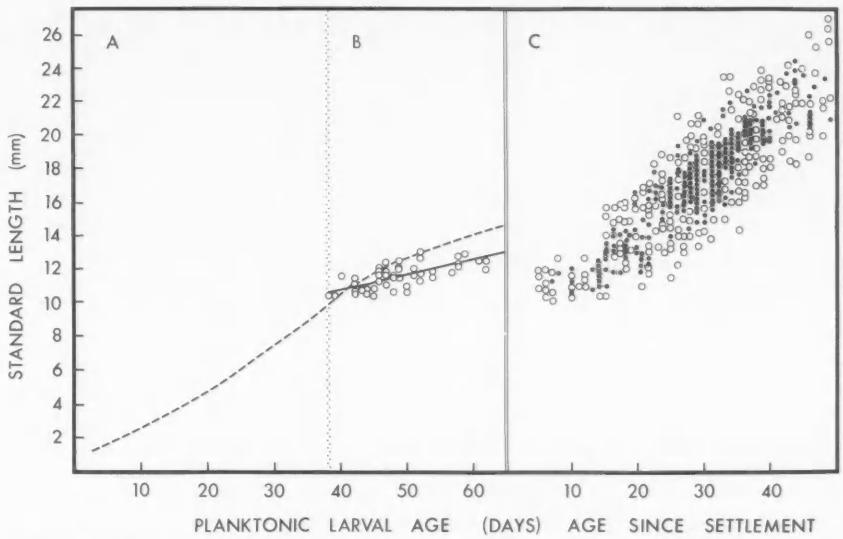

FIG. 4. Relationship between length and age for three phases in the life of bluehead wrasses. (A) Growth curve of larvae before a competent size is reached (back-calculated from the mean otolith radius for each age, $n = 25$ individuals, 10 with modal larval durations and 15 with extended durations combined); (B) growth curve of larvae after a competent size is reached was similarly back-calculated, as well as directly estimated from the change in size with increased larval duration of newly settled fish (solid line and open circles, $n = 47$); (C) growth rate after settlement was estimated by the relationship between the length of juveniles on the reef and their age since settlement (open circles, half-solid circles represent multiple points, $n = 694$).

directly from undisturbed natural populations that holds great promise for advancing our understanding of larval processes of both temperate and tropical fish species.

Planktonic Larval Duration

Many invertebrates are capable of extending their larval life after reaching a competent size in the absence of suitable settlement cues (see Jackson and Strathmann 1981). Whether fish larvae exhibit similar behavior has been an open question, since direct information on larval durations has been generally unavailable. Randall (1961) found in Hawaii that the larvae of convict surgeonfish, *Acanthurus triostegus*, which transformed after the main peak in settlement tended to be larger than those settling during the peak, and thus inferred that some larvae remain planktonic and continue to grow after reaching a size capable of settlement. Pearcy et al. (1977) observed occasional very large larvae of dover sole, *Microstomus pacificus*, well beyond normal settlement sizes in the plankton off of Oregon, and thus suggested that some larvae may be delaying settlement. Although the planktonic larval durations of a number of nonpelagic marine fishes have now been directly estimated

with the use of daily otolith increments, the sources of variability within species have not been examined (Brothers and McFarland 1981; Laroche et al. 1982; Victor 1982, 1983, 1984, 1986b; Brothers et al. 1983).

The length of the planktonic larval phase in the bluehead wrasse is extremely variable, with some individuals experiencing larval durations twice as long as the observed minimum. Furthermore, back-calculations of larval lengths indicate that those individuals with an extended larval duration reach a competent size at the same age as individuals with normal larval durations. While it has yet to be demonstrated, it is certainly plausible that size confers competency in most marine fish larvae. These results are in accord with the prediction of Jackson and Strathmann (1981) that coastal organisms with planktonic larvae subject to offshore mixing should have a competent period (delay period) greater than or equal to the precompetent period. The basis for this prediction is that species with long larval durations are subject to offshore dispersal of their larvae and therefore require long competent periods to allow for their return to a suitable habitat. Leis (1983) has recorded *Thalassoma* larvae in waters up to 1200 km east of the nearest coral reefs in the central Pacific, and I have found *Thalassoma* larvae several hundred kilometres east of the Galapagos Islands (the nearest reefs), confirming that wrasse larvae do disperse into offshore waters.

The methodology employed in this study can certainly be used in studies of temperate fish larvae as well. Estimates of the duration of the planktonic larval period of northern fishes are probably minimum estimates, since the potential for delayed metamorphosis has not been explored for these fishes. It is highly likely that at least some temperate fish species will be found to exhibit similar larval behavior. If they do, there may be important implications for recruitment success and subsequent population dynamics. Delayed metamorphosis can extend the season of settlement far beyond the window suggested by a narrow spawning season. Furthermore, if larvae are capable of remaining planktonic for extended periods, then short-term fluctuations in larval food supplies or oceanographic conditions may have less of an effect on future stock size than might otherwise be expected.

Larval Growth

Field estimates of the growth rates of larval fishes are becoming increasingly common as the daily otolith increment aging technique becomes more popular. Population estimates of growth rates are typically derived from length at age curves of wild-caught larvae. Alternatively, growth curves can be back-calculated from otolith widths, since the otolith length to fish length relationship tends to be close for marine fish larvae (correlation coefficients typically greater than 0.90, e.g. Lough et al. (1982) and Radtke and Dean (1982)). Campana and Neilson (1985) reported that linear fish length − otolith radius relationships are usual for juvenile fishes but that many larval fishes have a curvilinear relationship. However, other than for some flatfishes of the family Pleuronectidae, which undergo great morphological changes during metamorphosis (Laroche et al. 1982; Campana 1984), and the northern anchovy, *Engraulis mordax* (Methot 1981), the relationship has been reported to be linear (Methot 1981; Lough et al. 1982; Radtke and Dean 1982). I have found that for four species of planktonic tropical eastern Pacific wrasse larvae the fish length − otolith radius relationship is linear and close (correlation coefficients greater than 0.93, unpubl. data).

There is, at present, an absence of field data on growth rates of tropical fish larvae of nonpelagic species. My estimates of the growth rates of larval bluehead wrasses before competency ($0.18-0.26$ mm$\cdot$d^{-1}) are well within the range that has been reported for other marine fish larvae. These estimates typically lie between 0.1 and 0.3 mm$\cdot$d^{-1} (Boehlert 1981; Bailey 1982; Laroche et al. 1982; Lough et al. 1982), but can reach 0.55 mm$\cdot$d^{-1} in some northern anchovy (Methot and Kramer 1979).

The back-calculated estimate of the larval growth rate of bluehead wrasses during the period of delay was higher than the estimate derived from the change in size of new recruits with increased larval duration (0.13 versus 0.08 mm$\cdot$d^{-1}). The back-calculated estimate was, however, based on the equation for larval fish before competency, which are relatively fast-growing. As a result, it is probably an overestimate, since delaying larvae are growing relatively slowly and slow-growing fish are known to have larger otoliths (and therefore wider otolith increments) for their size than normal fish (Marshall and Parker 1982). This is corroborated by the evidence that new recruits with extended larval durations are smaller than predicted by the equation (Fig. 4). This method of estimation cannot be further refined without direct information on the effect of reduced growth rates on the fish length − otolith radius relationship.

Teleplanic (widely dispersing) invertebrate larvae often have a reduced growth rate during the period of delay after attaining a competent size (Scheltema 1971; Pechenik et al. 1984). In some planktonic gastropod larvae the cause of this reduction is considered to be either shifts in metabolism (a probable adaptation to limit size and shell weight for a prolonged oceanic migration) or food limitation in the open ocean (Pechenik et al. 1984). Since fish larvae have air bladders to control buoyancy, it is unlikely that increased size and weight carry a similar cost. The reduction in growth found in bluehead wrasse larvae after reaching a competent size could be a result of a shortage of food for larvae above a certain size, although the abruptness of the transition and the relatively small size of planktonic wrasse larvae (Leis and Rennis 1983; Richards and Leis 1984) argue against this explanation. Alternatively, once a competent size is reached, a larva may shift its behavioral repertoire from one that maximizes food intake and minimizes predation to one maximizing the chance of return to coastal waters, perhaps by altering patterns of vertical migration or some active movement. If this change results in lower food intake or increased energy expenditure, the rate of growth will be reduced. Since even the most fundamental aspects of the ecology of planktonic fish larvae are unknown, these questions must remain unanswered.

The first transition in the widths of otolith increments is often ascribed to settlement of the planktonic larva and has thus been used as a settlement mark (Panella 1980; Brothers et al. 1983). My results demonstrate that this transition can correspond to the onset of competency (the attainment of settlement size) rather than settlement itself. This finding reinforces the need for verification in the field of assumed life history markers in otolith increment sequences. Furthermore, the ability of fish larvae to delay metamorphosis demands that biogeographers recognize that the potential for delayed metamorphosis may be more relevant than average larval duration in studies assaying the role of dispersal ability in the biogeography of fishes.

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References

BAILEY, K. M. 1982. The early life history of the Pacific hake, *Merluccius productus*. Fish. Bull. 80: 589–598.

BOEHLERT, G. W. 1981. The effects of photoperiod and temperature on laboratory growth of juvenile *Sebastes diploproa* and a comparison with growth in the field. Fish. Bull. 79: 789–794.

BREDER, C. M., AND D. E. ROSEN. 1966. Modes of reproduction in fishes. Natural History Press, New York, NY. 941 p.

BROTHERS, E. B., AND W. N. MCFARLAND. 1981. Correlations between otolith microstructure, growth, and life history transitions in newly recruited French grunts [*Haemulon flavolineatum* (Desmarest), Haemulidae]. Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer 178: 369–374.

BROTHERS, E. B., D. MCB. WILLIAMS, AND P. F. SALE. 1983. Length of larval life in twelve families of fishes at One Tree Lagoon, Great Barrier Reef, Australia. Mar. Biol. 76: 319–324.

CAMPANA, S. E. 1984. Microstructural growth patterns in the otoliths of larval and juvenile starry flounder, *Platichthys stellatus*. Can. J. Zool. 62: 1507–1512.

CAMPANA, S. E., AND J. D. NEILSON. 1985. Microstructure of fish otoliths. Can. J. Fish. Aquat. Sci. 42: 1014–1032.

CHIA, F. S., AND M. E. RICE [ED.] 1978. Settlement and metamorphosis of marine invertebrate larvae. Elsevier, New York, NY. 290 p.

DOMANSKI, P. A. 1984. Giant larvae: prolonged planktonic larval phase in the asteroid *Luidia sarsi*. Mar. Biol. 80: 189–195.

HADFIELD, M. G. 1978. Growth and metamorphosis of planktonic larvae of *Ptychodera flava* (Hemichordata:Enteropneusta), p. 247–254. *In* F. S. Chia and M. E. Rice [ed.] Settlement and metamorphosis of marine invertebrate larvae. Elsevier, New York, NY.

JACKSON, G. A., AND R. R. STRATHMANN. 1981. Larval mortality from offshore mixing as a link between precompetent and competent periods of development. Am. Nat. 118: 16–26.

LAROCHE, J. L., S. L. RICHARDSON, AND A. A. ROSENBERG. 1982. Age and growth of a pleuronectid, *Parophrys vetulus*, during the pelagic larval period in Oregon coastal waters. Fish. Bull. 80: 93–104.

LASKER, R. [ED.] 1981. Marine fish larvae. University of Washington Press, Seattle, WA. 131 p.

LEIS, J. M. 1983. Coral reef fish larvae (Labridae) in the East Pacific barrier. Copeia 3: 826–828.

LEIS, J. M., AND D. S. RENNIS. 1983. The larvae of Indo-Pacific coral reef fishes. University of Hawaii Press, Honolulu, HI. 269 p.

LOUGH, R. G., M. PENNINGTON, G. E. BOLZ, AND A. A. ROSENBERG. 1982. Age and growth of larval atlantic herring, *Clupea harengus* L., in the Gulf of Maine – Georges Bank region based on otolith growth increments. Fish. Bull. 80: 187–199.

MARSHALL, S. L., AND S. S. PARKER. 1982. Pattern identification in the microstructure of sockeye salmon (*Oncorhynchus nerka*) otoliths. Can. J. Fish. Aquat. Sci. 39: 542–547.

METHOT, R. D. JR. 1981. Spatial covariation of daily growth rates of larval northern anchovy, *Engraulis mordax*, and northern lampfish, *Stenobrachius leucopsarus*. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 178: 424–431.

METHOT, R. D., AND D. KRAMER. 1979. Growth of northern anchovy, *Engraulis mordax*, larvae in the sea. Fish. Bull. 77: 413–423.

PANELLA, G. 1980. Growth patterns in fish sagittae, p. 519–560. *In* D. C. Rhoades and R. A. Lutz [ed.] Skeletal growth of aquatic organisms. Plenum Press, New York, NY.

PEARCY, W. G., M. J. HOSIE, AND S. L. RICHARDSON. 1977. Distribution and duration of pelagic life of larvae of dover sole, *Microstomus pacificus*; rex sole, *Glyptocephalus zachirus*; and petrale sole, *Eopsetta jordani*, in waters off Oregon. Fish. Bull. 75: 173–183.

PECHENIK, J. A., R. S. SCHELTEMA, AND L. S. EYSTER. 1984. Growth stasis and limited shell calcification in larvae of *Cymatium parthenopeum* during trans-Atlantic transport. Science (Wash., DC) 224: 1097–1099.

RADTKE, R. L., AND J. M. DEAN. 1982. Increment formation in the otoliths of embryos, larvae, and juvenile of the mummichog, *Fundulus heteroclitus*. Fish. Bull. 80: 201–215.

RANDALL, J. E. 1961. A contribution to the biology of the convict surgeonfish of the Hawaiian Islands, *Acanthurus triostegus sandvicensis*. Pac. Sci. 15: 215–272.

RICHARDS, W. J., AND J. M. LEIS. 1984. Labroidei: development and relationships, p. 542–547. *In* H. G. Moser [ed.] Ontogeny and systematics of fishes. Allen Press, Lawrence, KS.

RICHMOND, R. H. 1985. Reversible metamorphosis in coral planula larvae. Mar. Ecol. Prog. Ser. 22: 181–185.

SALE, P. F. 1980. The ecology of fishes on coral reefs. Oceanogr. Mar. Biol. Annu. Rev. 18: 367–421.

SCHELTEMA, R. S. 1971. Larval dispersal as a means of genetic exchange between geographically separated populations of shallow-water benthic marine gastropods. Biol. Bull. 140: 284–322.

SCHELTEMA, R. S., AND I. P. WILLIAMS. 1983. Long-distance dispersal of planktonic larvae and the biogeography and evolution of some Polynesian and Western Pacific mollusks. Bull. Mar. Sci. 33: 545–565.

VICTOR, B. C. 1982. Daily otolith increments and recruitment in two coral reef wrasses, *Thalassoma bifasciatum* and *Halichoeres bivittatus*. Mar. Biol. 71: 203–208.

1983. Settlement and larval metamorphosis produce distinct marks on the otoliths of the slippery dick, *Halichoeres bivittatus*, p. 47–52. *In* M. L. Reaka [ed.] The ecology of deep and shallow coral reefs. Office of Undersea Research, U.S. Department of Commerce, Washington, DC.

1984. Coral reef fish larvae: patch size estimation and mixing in the plankton. Limnol. Oceanogr. 29: 1116–1119.

1986a. Larval settlement and juvenile mortality in a recruitment-limited coral reef fish population. Ecol. Monogr. (In press)

1986b. The duration of the planktonic larval stage of one hundred species of Pacific and Atlantic wrasses (Family Labridae). Mar. Biol. 90: 317–326.

An Experimental and Statistical Approach to the Question: Is CPUE an Index of Abundance?

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Richards, L. J., and J. T. Schnute. 1986. An experimental and statistical approach to the question: Is CPUE an index of abundance? Can. J. Fish. Aquat. Sci. 43: 1214–1227.

Catch per unit effort (CPUE) is often assumed to be an index of stock abundance. Here we present an experiment and a general model for testing this assumption. We used the submersible *Pisces IV* to make visual estimates of reef-fish density in the Strait of Georgia, British Columbia. These density estimates were compared with CPUE estimates obtained by research angling at the same sites. Our model allows for no relationship between CPUE and density, strict proportionality, and departures from proportionality at either low or high densities or both. We performed the analysis using an ordinary least squares (OLS) model and an errors-in-variables (EV) model that includes error in both CPUE and density. For the dominant species (quillback rockfish, *Sebastes maliger*), the relationship was one of strict proportionality. However, CPUE was a poor abundance index when data were combined across species. In these cases the OLS and EV models generally resulted in different conclusions; the EV model explained a low CPUE at high density by allowing for error in the density measurement.

On présume souvent que les prises par unité d'effort (PPUE) constituent un indice de l'abondance des stocks. Nous présentons ici une expérience et un modèle général afin de vérifier cette hypothèse. Nous nous sommes servis du submersible *Pisces IV* pour faire des estimations visuelles de la densité des poissons de récifs dans le détroit de Géorgie, en Colombie-Britannique. On a comparé ces estimations de la densité avec les estimations de PPUE obtenues en pratiquant la pêche à la ligne à des fins de recherche aux mêmes endroits. Notre modèle ne permet pas de relation entre les PPUE et la densité, de stricte proportionnalité et d'écart par rapport à cette proportionnalité à des densités faibles ou fortes ou aux deux. Nous avons fait l'analyse en employant un modèle par la méthode ordinaire des moindres carrés (MOMC) et un modèle d'erreurs dans les variables (EV) qui englobe l'erreur dans les PPUE et dans la densité. Pour l'espèce dominante (le sébaste à dos épineux, *Sebastes maliger*), la relation était de stricte proportionnalité. Cependant, les PPUE constituaient un pauvre indice d'abondance lorsque les données étaient combinées entre espèces. Dans ces cas, les modèles MOMC et EV ont abouti en général à des conclusions différentes; le modèle d'EV expliquait de faibles PPUE à une densité élevée en tenant compte de l'erreur dans la mesure de la densité.

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One of the common assumptions in fisheries research is that relative stock abundance can be estimated from a knowledge of catch and fishing effort for that stock. The simplest form of this assumption is

$$U = qA$$

where U is the catch per unit of effort (CPUE), q is the catchability coefficient, and A is a measure of abundance, such as stock density (Ricker 1940, 1944; review by Paloheimo and Dickie 1964). In practise, however, the relationship between U and A is usually more complicated than the strict proportionality indicated above. The catchability q may itself be a function of other factors, such as the area swept by the gear, the behavior of fish and fishermen, and fish density (Gulland 1964; Rothschild 1977). Consequently, for example, U may appear asymptotically related to A (reviews by Peterman and Steer 1981; Bannerot and Austin 1983).

Here we develop a general model for the relationship between CPUE and abundance. Our analysis allows several distinct forms for the relationship and employs statistical tests to decide among them. Strict proportionality and an asymptotic relationship are treated as special cases. Furthermore, our model addresses a problem inherent in any statistical attempt to determine a relationship between U and A. Both quantities are measured with error; consequently, the usual least squares estimates based on error in U alone are inappropriate. We formulate a more realistic errors-in-variables model and apply it to a case in which an estimate of the ratio of variances in U and A is possible because of replicated observations.

We illustrate the model's application with data from the inshore rockfish fishery in the Strait of Georgia, British Columbia. We used the submersible research vessel *Pisces IV* to make direct counts of reef fish, and we compared these counts with CPUE measurements obtained by angling from a surface vessel. The experiment was part of an assessment program for Strait of Georgia groundfish stocks that are jointly exploited by commercial handline and recreational fisheries.

Experimental Methods

Site Locations

The study was conducted at 14 sites (Fig. 1) in the northeast

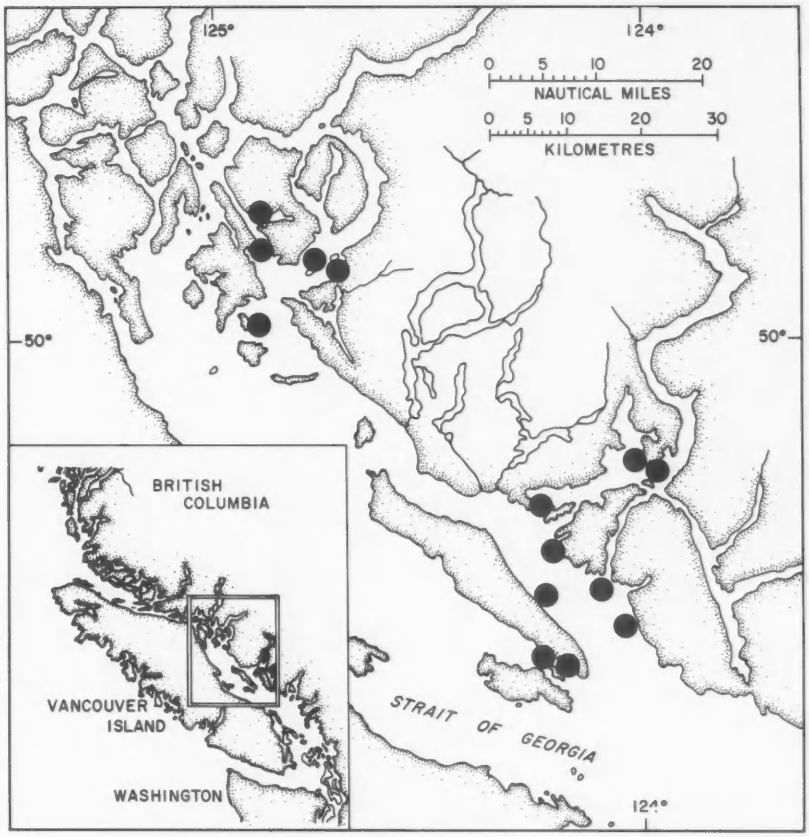


FIG. 1. *Pisces IV* dive locations in the Strait of Georgia, British Columbia.

section of the Strait of Georgia (50°N, 124°W). Subject to access limitations, sites were selected randomly (Richards et al. 1985) from numbered blocks 1′N by 1′W within minor statistical areas 15 (five sites) and 16 (nine sites). The particular choice of statistical areas was based on the fact that rockfish landings per unit effort for the recreational fishery had been high in these areas. Consequently, the observed range in stock abundance could be expected to include abundances near the maximum generally encountered in the fishery. In fact, the 14 sites represented a spectrum of abundances from low to high.

Research Angling Methods

Research angling was conducted in August 1984 from the M/V *Keta*, a 12-m research seiner, using recreational angling gear. Additional fishing was conducted at the times and locations of the submersible dives in October (from a 7-m aluminum skiff) and November (from a 3-m fibreglass whaler). We used trolling rods and reels and 12-cm frozen bait herring.

Three depth intervals were fished at most sites: 5–40, 41–70, and 71–100 m. There were generally two or three anglers, each with one line. Approximately 1 h of fishing effort on each line was spent at each depth interval for each day of fishing at each site. Most recreational fishing is restricted to the first two depth intervals, and commercial rockfish fishing occurs in all three depth intervals. However, the first depth interval could not be adequately covered by *Pisces IV*, and the number of fish counted from *Pisces IV* below 70 m was too low to provide adequate density estimates. We report here only on research angling and *Pisces IV* data from the middle depth interval, 41–70 m.

In addition to catch and effort data, we recorded sea surface conditions, tidal phase, and time of day as a check for other factors that might influence CPUE. A new record was begun for each hour at a site or whenever sea surface conditions changed. Records were not counted unless we remained at a site under similar sea surface conditions for at least a 10-min period. Raw data and further methodological details are available in Richards et al. (1985).

Submersible Methods

A basic discussion of the *Pisces IV* submersible is presented by Mackie and Mills (1983). Raw data, including descriptions of the sea bottom at each site, are available in Richards and Cass (1985).

Pisces IV carries a pilot and two observers. A dive began with a direct descent to approximately 150 m. The pilot then drove the submersible to within 2 m of the bottom and began the ascent. We had determined 2 m from the bottom to be an appropriate distance for counts under most conditions of visibility. Ascent speed varied according to habitat complexity and pilot preference, although differences were minor. The transect ended at an upper depth of about 20 m. The process

was repeated for additional transects at all but two sites. Although the distance between replicate transects was not measured, it was probably much greater than the visibility. The dominant rockfish species typically show little movement (Mathews and Barker 1983), and it was unlikely that fish were counted more than once. All dives were completed during daylight hours with generally one morning and one afternoon dive.

One observer was stationed on each side of the submersible. Because of the port positions, each observer scanned 90° to one side of the submersible path. There was little or no overlap in their observations. Counts made by each observer were summed to obtain the total for a transect. Fish that swam across the submersible path were immediately described to the other observer to avoid double counts. Observers counted all fish except small and/or cryptic species, such as sculpins, gobies, and flatfishes, or midwater species, such as herring and hake. These species were difficult to count and were rarely taken by angling gear.

Size of rockfish and lingcod was determined by comparison with a 60-cm rod, marked at 10-cm intervals, that hung in front of each port. As it was sometimes possible to align a fish directly with the rod, observers learned to estimate fish size by noting changes in apparent size for fish that remained motionless as the submersible passed. The accuracy of size estimates was believed to be within 10%.

Horizontal visibility (±0.5 m, the distance beyond which objects no longer could be distinguished) and slope (±10° from horizontal) were visually estimated for each 10-m change in depth. The recorded values were decided by a consensus among the pilot and observers. There was little disagreement over these estimates. Visibility was generally between 3 and 5 m until surface light became a factor at a depth of 30−40 m, where visibility increased to as much as 8 m. The sea bottom area covered by each observer was calculated as the visibility multiplied by the distance travelled, estimated from the ratio of the vertical depth change to the sine of the slope. Although there may be bias in these estimates, the bias should at least be consistent throughout the experiment, as the same two observers participated in all dives.

A general problem with the use of submersibles has been to quantify fish abundances, especially in complex fish communities that include schooling species. Schooling species are not an important component of the reef-fish communities in our study area. In the Strait of Georgia, the dominant reef species are lingcod (*Ophiodon elongatus*) and various rockfish (*Sebastes*), mainly copper rockfish (*S. caurinus*), quillback rockfish (*S. maliger*), yelloweye rockfish (*S. ruberrimus*), tiger rockfish (*S. nigrocinctus*), and greenstriped rockfish (*S. elongatus*) (Hart 1973). As these species tend to be solitary and demersal and, from our experience, do not appear to alter their behavior in the presence of the submersible, they can be studied effectively by this approach.

Analytical Methods

Modeling

Peterman and Steer (1981) discussed a general model for relating population density to CPUE. In particular, their model allows for gear saturation, that is, no significant increase in CPUE as the density increases above some high level. For reasons explained below, our data require a model with even greater flexibility. If U represents the CPUE (fish per line per hour) and D an index of density (fish per square metre), then our model consists of the two conditions

$$\text{(1a)}\quad U = (p + qD)/(1 + rD) \quad \text{if } D > -p/q$$

$$\text{(1b)}\quad U = 0 \quad \text{if } D \leq -p/q$$

where p, q, and r are parameters constrained so that

$$\text{(2a)}\quad qr \geq 0$$

$$\text{(2b)}\quad q \geq pr.$$

The curve (1a) crosses the U-axis ($D = 0$) where $U = p$ and the D-axis ($U = 0$) where $D = -p/q$. When $pq < 0$, U in (1a) is negative for positive values of D immediately below $-p/q$. The restriction (1b) eliminates this biological impossibility by truncating the curve at $U = 0$. When $r \neq 0$, the curve (1a) approaches the value $U = q/r$ asymptotically as D becomes large. Condition (2a) guarantees that this asymptotic value (if it exists) is positive. Condition (2b) forces the derivative

$$dU/dD = (q - pr)/(1 + rD)^2$$

to be positive, so that the CPUE does not decrease as the density index increases.

Unlike the model of Peterman and Steer (1981), our model (1) admits the possibility that $p \neq 0$. When $pq > 0$, the CPUE is not 0 when the density index is 0. This phenomenon might occur, for example, because the attraction of the bait produces a high CPUE even at low population densities. Consequently, the curve relating U to D does not approach the origin continuously, but instead drops very suddenly to 0 at low levels of D. The model (1) can be considered a continuous extension of such a curve to the point $D = 0$. A second possibility is that $pq < 0$. The CPUE then becomes 0 even when fish are present, as indicated in (1b). This might occur, for example, if the fish present are not susceptible to the bait.

From model (1), several potential relationships between D and U can be identified. These correspond to restrictions on the parameters listed in the following table, where "0" and "*" indicate zero and nonzero values, respectively:

Case No.	p	q	r
1	0	*	0
2	0	*	*
3	*	0	0
4	*	*	0
5	*	*	*

These are five of the eight (2^3) possibilities that p, q, and r are either zero or nonzero; the remaining three are not biologically meaningful. Figure 2 shows typical curve forms for each of the five cases. Case 1 corresponds to the classical assumption that CPUE indexes (i.e. is proportional to) the density. Case 2 is similar in form at low densities but asymptotic at high densities. Case 3 is essentially a nonrelationship; CPUE is a constant, independent of density. In case 4 the relationship is linear, but distinctly not proportional, due to the fact that the line does not pass through the origin. In case 5 the relationship is asymptotic (as in case 2), but (as in case 4) it does not pass through the origin. Case 5 becomes a step function near the constraint (2b), as will be shown below.

An alternative interpretation of model (1) is obtained by focussing on the ratio U/D, a measure of catchability. The

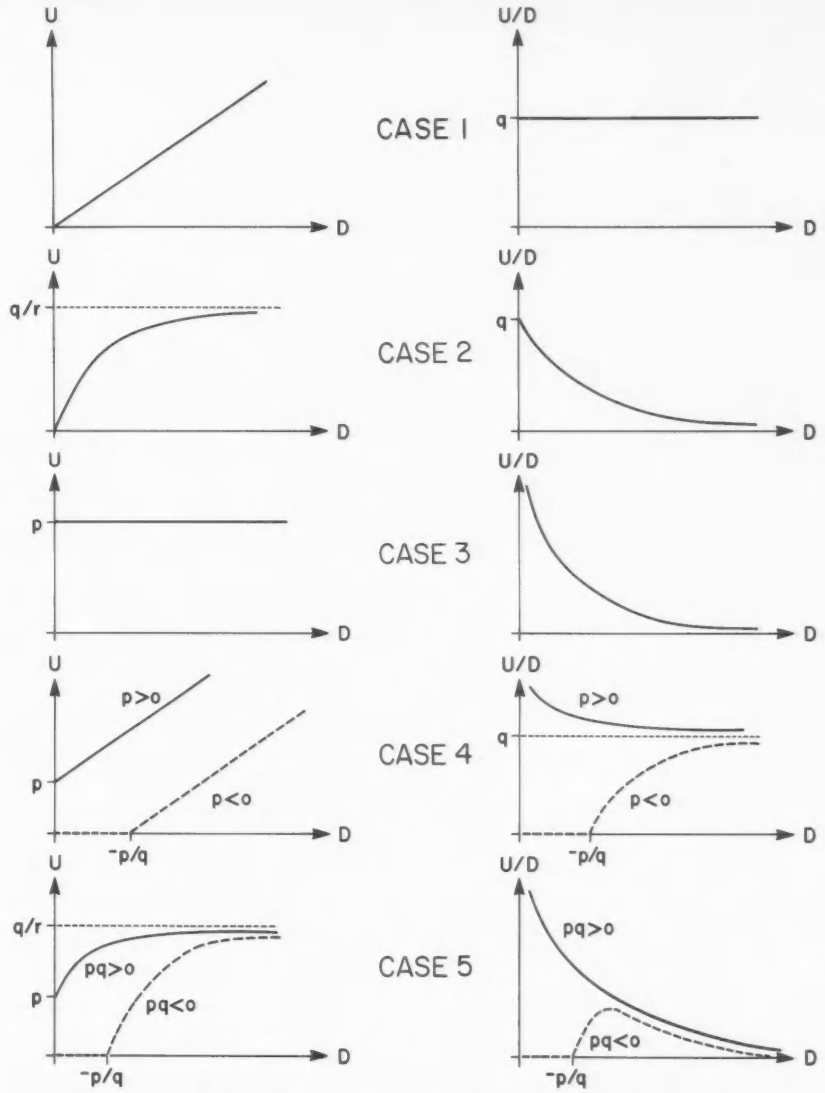


FIG. 2. Typical curve forms for five cases of the relationship between CPUE (U, fish·line^{-1}·h^{-1}) and the density index (D, fish·m^{2}), and the corresponding relationship between the ratio U/D, a measure of catchability, and D. Parameter values are indicated where curves cross the axes. Multiple solutions are shown if the curve form depends on parameter values.

right-hand panels of Fig. 2 show typical curve forms. Case 1 is characterized by the fact that this ratio is constant. In case 2, catchability decreases to 0 as D becomes large. In case 3, since U is constant, the catchability U/D is large for small D and small for large D. Case 4 corresponds to a catchability that increases or decreases (when p is negative or positive, respectively) toward the limiting value q as D increases. Case 5 combines the features of case 4 for small D and case 2 for large D. In this case, when $pq < 0$, the catchability is small for either small or large D and is maximum at some intermediate density D. Explicitly, when $pq < 0$, U/D is maximized at the density

$$D_m = \{[pr(pr - q)]^{1/2} - pr\}/(qr).$$

The parameters p, q, and r in (1) have simple biological interpretations, at least when they are all positive. Case 1, namely

$$U = qD, \quad (3)$$

has only the single parameter q with units square metres per line per hour. This is a catchability coefficient that intuitively represents the effective area fished in 1 h with one line. The second parameter p (fish per line per hour) approximates U when D is near 0 and represents a limiting CPUE at low densities due, for example, to bait attraction. Finally, the third parameter r (square metres per fish) induces asymptotic behavior; $1/r$ is the density at which the CPUE is reduced to half the

level it would be if r were 0. These interpretations need to be modified if some parameters are negative. For example, Fig. 2 shows the significance of the density $-p/q$ when $pq < 0$.

Statistical Error and Parameter Estimation

Statistical error associated with the application of model (1) is complicated for two reasons. First, in practice the error is not homoscedastic. Second, and more seriously, both variables U and D are measured with error. Recent papers (e.g. Uhler 1980; Walters and Ludwig 1981; Ludwig and Walters 1981; Schnute 1984) have warned that the errors-in-variables problem can have serious consequences for analysis of fisheries data. Fortunately, in the present context we have the extra information needed to treat the problem properly, namely an independent estimate of the ratio of errors in measuring U and D. This is available because, at most sites, research angling was repeated and underwater density measurements were made along more than one transect.

To be precise, let d_i $(i = 1,\ldots,k)$ represent the observed density index at the ith site and let D_i be the corresponding true, but unobserved, density index. Thus, D_i represents the theoretical visual density that would be obtained from infinitely many transects at site i. Similarly, let u_i be the observed CPUE at the ith site with a corresponding true value U_i. Then the model consists of the following assumptions:

$$\text{(4a)}\quad U_i = (p + qD_i)/(1 + rD_i) \qquad \text{if } D_i > -p/q$$

$$\text{(4b)}\quad U_i = 0 \qquad \text{if } D_i \le -p/q$$

$$\text{(5)}\quad d_i = D_i + \sigma f_i \delta_i$$

$$\text{(6)}\quad u_i = U_i + \tau g_i \epsilon_i$$

where δ_i and ϵ_i are independent normal random variables with mean 0 and variance 1. Assumptions (4a) and (4b) state that the true values D_i and U_i precisely satisfy model (1). Assumption (5) describes how the observed d_i is determined from D_i and a random measurement error δ_i. The quantity σf_i in (5) is the standard deviation of d_i, where σ is a fixed parameter and the quantities f_i $(i = 1,\ldots,k)$ are weighting factors, presumed known, that compensate for heteroscedastic variance. These are discussed further in the next paragraph. Similarly, (6) describes the relationship between observed u_i and predicted U_i, where ϵ_i is a random error, τg_i is a standard deviation, and g_i is a weighting factor, presumed known.

The details of computing site mean observations (d_i, u_i) and weights (f_i, g_i) are given in the Appendix. The calculations there are peculiar to the structure of our data. We examine various alternatives and select the approach that best renders the variance homoscedastic. We also obtain an estimate of the ratio

$$\text{(7)}\quad \lambda = \tau/\sigma$$

needed for consistent likelihood estimates of the model's parameters. Notice that the quantities f_i, g_i, and λ all describe *relative* error. The weights (f_i, g_i) pertain to relative error differences among sites, and λ describes the overall relative error between CPUE and density. A measure of absolute error is not required to apply the model.

The likelihood function L associated with the model (4)−(6) is simply the product of normal likelihoods for d_i and u_i $(i = 1,\ldots,k)$, that is

$$\text{(8)}\quad L = (2\pi\sigma\tau)^{-k}\left[\prod_{i=1}^{k}(f_i g_i)^{-1}\right]\exp\left[-\frac{1}{2}\sum_{i=1}^{k}(\delta_i^2 + \epsilon_i^2)\right].$$

The product Π in (8) comes from assumptions (5) and (6) that the standard deviations of d_i and u_i are proportional to f_i and g_i, respectively. Thus, (8) contains the factors $(\sigma f_i)^{-1}$ and $(\tau g_i)^{-1}$ with $i = 1,\ldots,k$. Define

$$A = -\log L - k\log(2\pi) - \sum_{i=1}^{k}\log(f_i g_i),$$

that is, let A represent the negative log likelihood except for a constant independent of parameters. Then it follows from (4a) and (5)−(8) that

$$\text{(9)}\quad A = k\log(\lambda\sigma^2) + \frac{1}{2}\sigma^{-2}\sum_{i=1}^{k}[(d_i - D_i)/f_i]^2 + \frac{1}{2}(\lambda\sigma)^{-2}\sum_{i=1}^{k}\{[u_i - (p + qD_i)/(1 + rD_i)]/g_i\}^2.$$

The unknown parameters in (9) are p, q, r, σ, and the true densities $D_1, D_2,\ldots,D_k$. Thus, the function A depends on $4 + k$ parameters, that is

$$A = A(p,q,r,\sigma,D_1,\ldots,D_k).$$

These parameters can be estimated by minimizing A (and so maximizing L) subject to the constraints (2) and

$$\text{(10)}\quad D_i \ge 0 \text{ for } i = 1,\ldots,k.$$

In addition, (9) needs one minor modification. When $pq < 0$ and $D_i < -p/q$, the expression

$$(p + qD_i)/(1 + rD_i)$$

in (9) should be redefined 0 to be consistent with (4b).

With the above qualifications, the model parameters can be estimated by a constrained minimization of A. For example, our analysis below uses the simplex search method (Nelder and Mead 1965; O'Neill 1971) as implemented by Mittertreiner and Schnute (1985). Given the remaining parameters, the maximum likelihood estimate $\hat{\sigma}$ (obtained from the equation $\partial A/\partial\sigma = 0$) is given directly by

$$\text{(11)}\quad 2k\hat{\sigma}^2 = \sum_{i=1}^{k}[(d_i - D_i)/f_i]^2 + \lambda^{-2}\sum_{i=1}^{k}\{[u_i - (p + qD_i)/(1 + rD_i)]/g_i\}^2.$$

This reduces the number of parameters for the search to $3 + k$. By analogy with the linear errors-in-variables model (Kendall 1980, p. 121−122), $\hat{\sigma}^2$ in (11) is not a statistically consistent estimator for the true parameter σ^2. A revised estimate $\tilde{\sigma}^2$, approximately corrected for both consistency and bias, is given by

$$\text{(12)}\quad \tilde{\sigma}^2 = [2k/(k - 3)]\,\hat{\sigma}^2.$$

In (12) the factor "2" corrects for consistency, and the factor "$k/k-3$" allows for the loss of 3 df due to the estimation of p, q, and r in case 5. The df loss in cases 1−4 is either 1 or 2, depending on the number of parameters estimated.

Hypothesis Testing

Cases 1−5 of model (4) can be obtained by suitable restrictions of the parameters p, q, and r. In general, let H_0 be the null hypothesis that a model with h_0 parameters is correct, and let H_1 be the alternative hypothesis that a more general model with $h_1 > h_0$ parameters applies. Let A_0 and A_1 be the minimum values of A obtained under H_0 and H_1, respectively,

and define

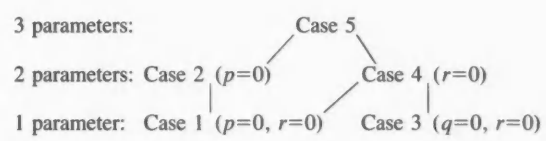
$$B = 2(A_0 - A_1). \quad (13)$$

Then, assuming that H_0 is true, it follows from the likelihood ratio test that

$$B \sim \chi^2 (h_1 - h_0) \quad (14)$$

approximately for large k. Thus, the upper 95% point for the χ^2 distribution with $(h_1 - h_0)$ df can be used as an approximate critical level for the statistic B; a larger value of B means that H_0 should be rejected.

To describe a methodology for choosing the appropriate case of the five possible, it is necessary to specify a precise testing procedure. Definition of such a procedure is made complicated by the fact that the cases are organized in the hierarchy represented below:



Cases connected by lines in this diagram are comparable, that is, the lower one can be considered a null hypothesis with the upper one as an alternative hypothesis. Notice that cases 2 and 3 are not comparable.

There are two prevailing schools of thought in selecting a case from such a range of possibilities: bottom-up (successively adding parameters to simpler models) and top-down (successively eliminating parameters from more complex models). To accommodate the slightly complex hierarchy above, we are forced to choose the top-down approach. Specifically, we select a case by the following series of steps.

Step 1: Find parameter estimates and minimum values of A for all five cases.

Step 2: Cases 2 and 4 each contain two free parameters. Reject the case (of these two) with the highest minimum value of A.

Step 3: If case 2 is rejected in step 2, go to step 4. If case 4 is rejected, then apply the method of (13) and (14) to test case 2 as the null hypothesis against case 5. If case 2 is rejected, then accept case 5 and stop. Otherwise, apply (13) and (14) to test case 1 as the null hypothesis against case 2. If case 1 is rejected, accept case 2 and stop; otherwise, accept case 1 and stop.

Step 4: If case 2 is rejected in step 2, then apply (13) and (14) to test case 4 as the null hypothesis against case 5. If case 4 is rejected, then accept case 5 and stop. Otherwise, use (13) and (14) to compare the better (i.e. lower minimum A) of cases 1 and 3 with case 4. If this case is rejected, accept case 4 and stop; otherwise, accept the better of cases 1 and 3 and stop.

This entire procedure is somewhat informal and approximate, particularly since the likelihood ratio test (13) and (14) is only a large sample approximation. Furthermore, as shown in the discussion of results below, a case may be acceptable on the basis of its A value and yet unacceptable based on the associated residuals. An alternative to hypothesis testing is to prepare a table of probability levels for rejecting various cases in favor of others. These can then be used in a Bayesian sense to assess the relative validity of the five possible cases. We apply this idea, too, in our discussion of results.

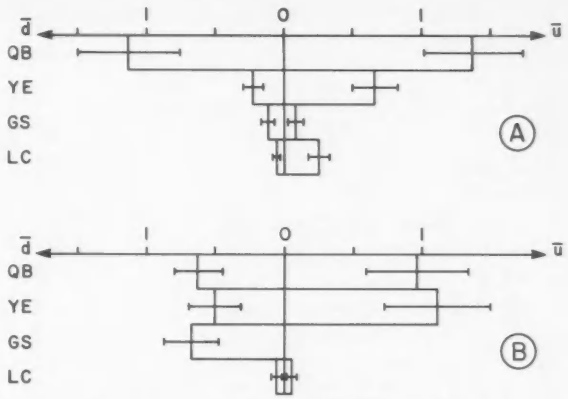


FIG. 3. Overall mean density ($\bar{d}$, fish·(100 m^2)$^{-1}$) and overall mean CPUE ($\bar{u}$, fish·line^{-1}·h^{-1}) for the major species that were observed or caught over (A) the 41–70 m depth interval and (B) the 71–100 m depth interval. QB, quillback rockfish; YE, yelloweye rockfish; GS, greenstriped rockfish; LC, lingcod.

TABLE 1. Estimates of σ, τ, and λ for the six data sets, based on multiple measurements of density and CPUE at some sites.

Data set	σ	τ	λ
1. Aug QB	0.64882	2.0050	3.0902
2. Aug RF	0.50192	2.1980	4.3792
3. Aug RF/LC	0.48629	2.2962	4.7218
4. Sea QB	0.64882	1.8801	2.8977
5. Sea RF	0.50192	2.0288	4.0421
6. Sea RF/LC	0.48629	2.1356	4.3916

Results

Data Standardization

Research angling data at each site included effort, depth, fishing conditions, fish species in the catch, and fish size. Submersible data at each site included area covered, depth, fish species counted, and fish size. A standardization process was required prior to comparison of these data sets. For example, fish size was not consistent between research angling and submersible data. The minimum size of fish susceptible to the angling gear was approximately 15 cm fork length (FL) for greenstriped rockfish and 20 cm FL for other rockfish species. To compensate for angling selectivity, densities of fish observed from *Pisces IV* were calculated for rockfish larger than the minimum susceptible sizes only. All observed lingcod were of a susceptible size.

Quillback rockfish was the dominant species both observed from *Pisces IV* and caught by research angling over the 41–70 m depth interval (Fig. 3A). Most rockfish did not appear to alter their behavior as the submersible passed, and we considered the observed densities to be representative of differences in relative abundance of the rockfish species. Lingcod were occasionally disturbed by the submersible, however, and so lingcod densities may be underestimated. Sample sizes were small for species other than quillback rockfish, and it was necessary to combine data over species prior to application of the model. We divided the submersible and research angling data into three sets to include progressively more species: (1)

TABLE 2. Parameter estimates and minimum A values for the six data sets and five cases of the EV model. Case 5 has two solutions for some data sets.

Data set	Case	p	q	r	σ	τ	min A
1. Aug QB	1	—	107	—	0.120	0.372	−21.046[a]
	2	—	109	0.6	0.120	0.372	−21.051
	3	1.86	—	—	0.559	1.727	9.646
	4	−0.25	123	—	0.114	0.354	−22.073
	5	−0.73	196	17.7	0.106	0.329	−23.525
2. Aug RF	1	—	179	—	0.258	1.129	−2.341[a]
	2	—	354	56.4	0.240	1.049	−3.802
	3	3.07	—	—	0.350	1.534	3.788
	4	0.85	122	—	0.248	1.087	−3.095
	5a	0.61	265	40.3	0.236	1.032	−4.131
	5b	4.55	−408	−91.9	0.206	0.900	−6.871[b]
3. Aug RF/LC	1	—	185	—	0.271	1.281	−0.562[a]
	2	—	409	65.2	0.252	1.192	−2.014
	3	3.38	—	—	0.329	1.555	3.307
	4	1.35	103	—	0.249	1.176	−2.279
	5a	1.13	242	35.9	0.241	1.136	−2.974
	5b	4.60	−379	−82.3	0.222	1.046	−4.648[b]
4. Sea QB	1	—	107	—	0.181	0.525	−14.874[a]
	2	—	116	4.0	0.181	0.523	−14.946
	3	1.66	—	—	0.602	1.744	11.538
	4	−0.03	105	—	0.181	0.525	−14.889
	5	−1.35	325	50.6	0.166	0.482	−16.737
5. Sea RF	1	—	187	—	0.274	1.107	−2.121[a]
	2	—	346	65.2	0.254	1.027	−3.777
	3	2.64	—	—	0.366	1.478	4.238
	4	1.43	58	—	0.264	1.067	−2.947
	5a	0.65	230	40.6	0.249	1.007	−4.200
	5b	10.83	−1999	−462.4	0.237	0.957	−5.322
6. Sea RF/LC	1	—	183	—	0.271	1.279	−0.661
	2	—	397	77.0	0.235	1.108	−3.814
	3	2.88	—	—	0.306	1.447	2.048
	4	1.80	47	—	0.230	1.087	−4.240[a]
	5a	1.18	188	32.7	0.221	1.044	−5.135
	5b	39.84	−8153	−1800.0	0.225	1.060	−4.785

[a]Case selected by both hypothesis and residual tests.
[b]Case selected by the hypothesis testing sequence.

quillback rockfish data only (QB), (2) all rockfish data (RF), and (3) all rockfish and lingcod data (RF/LC).

Quillback rockfish densities were much lower over the 71−100 m depth interval than at shallower depths (Fig. 3B). There were no differences in density among quillback, yelloweye, and greenstriped rockfish at this depth interval. Quillback and yelloweye rockfish were caught at similar low rates, with greenstriped rockfish totally absent from the catch. As discussed in the methods section above, data from this depth were excluded from further analyses.

RF/LC CPUE was significantly reduced by rough sea surface conditions (Richards et al. 1985), and it was necessary to standardize the CPUE data for this factor prior to testing for a relationship between CPUE and density. As the choice of a standardization procedure could affect the modeling results, we applied two methods for comparision. For the first method (Aug), we used data from August only, as poor weather occurred mainly during the October and November fishing periods. For the second method (Sea), we used data from all months but excluded records with sea surface conditions described as chop. Neither sea surface conditions, time of day, nor tidal phase had a significant effect on CPUE when data were standardized by these methods (Kruskal−Wallis tests, $p > 0.10$). In total, there were six data sets for analysis, formed from three combinations of species (QB, RF, and RF/LC) and two methods of standardization of CPUE data (Aug and Sea).

Data Compilation and Calculation of λ

As explained above in the analytical methods section, parameter estimation requires prior knowledge of certain variance weights (f_i, g_i) and the variance ratio λ. These can be estimated from the data because replicate transects were conducted by *Pisces IV* at most sites and research angling times were generally divided into more than one period. Details of these calculations are given in the Appendix.

With the six data sets, there are three estimates of σ depending on species combination and six estimates of τ depending on species and month or sea conditions. These give

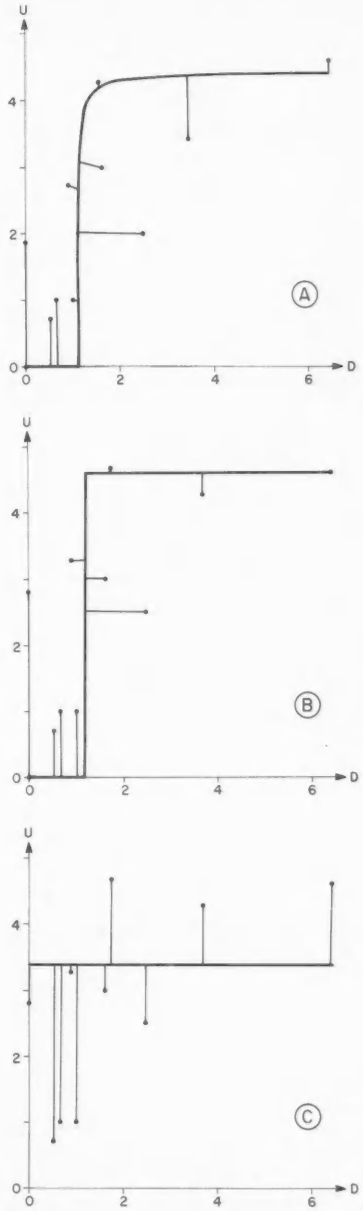


FIG. 4. Relationship between CPUE (U, fish·line^{-1}·h^{-1}) and the density index (D, fish·(100 m^2)$^{-1}$) for cases that are rejected on the basis of residuals. The thin lines connect data points to the corresponding EV estimates of density and CPUE on the curve. (A) Data set 2, Aug RF, case 5b; (B) data set 3, Aug RF/LC, case 5b; (C) data set 3, Aug RF/LC, case 3.

six estimates of the variance ratio λ in (9), as shown in Table 1. Notice that, as far as variances are concerned, only the weights f_i (from (A.3)), g_i (from A.15), and the ratio λ (from (9), (A.6), and (A.14)) are carried into the likelihood calculation. As mentioned earlier, these all pertain to relative variances. Thus, whatever the approximations used here, they enter the final calculation only in a weak sense; we do not need to commit ourselves to absolute magnitudes of variance.

Data Analysis

Parameter estimates for the errors-in-variables (EV) model obtained by the simplex search method (Mittertreiner and Schnute 1985) are presented in Table 2 for the five cases of the six data sets. Multiple solutions are possible, and we illustrate this fact by presenting more than one solution for case 5 in data sets 2, 3, 5, and 6. Otherwise, the table reports only the best solution for each case. Table 3 is similar to Table 2, but contains ordinary least squares (OLS) parameter estimates, assuming that $\sigma=0$ in (5). Thus, the estimates in Table 3 are found by minimizing the sum of squares

$$(15)\quad S(p,q,r) = \sum_{i=1}^{n} \{[u_i - (p_i + qd_i)/(1 + rd_i)]/g_i\}^2$$

where $g_i = 1/e_i$, as in (A.15). This sum can be compared with the third term of (9). Percentage significance levels for all possible hypothesis tests are presented in Table 4. These are computed from the χ^2 statistic B in (13) for the EV model and the usual F-statistic association with the sum of squares S for the OLS model.

In the EV model, minimum A values (Table 2) are an index of goodness-of-fit for cases within a data set. For example, it is obvious that case 3 can be rejected for all data sets on the basis of high A values. Values of σ and τ are also higher for case 3. Since case 3 corresponds to constant CPUE, its rejection implies that there is a relationship between CPUE and density in the data. The exact form of the relationship is less clear, as differences in minimum A among the other cases tend to be minor.

Minimum A values can also provide a rough comparison among data sets. The A values for single-species data sets (1 and 4, QB only) are considerably lower than the values for the other, multispecies data sets. The fit of the model is decreased by combining data across species, probably due to species-specific behaviors that result in differences among species in observation or catchability. The decrease in fit is reflected by higher values for σ and τ.

On the basis of the hypothesis testing sequence outlined above, accepted solutions for the EV model are case 1 for data sets 1, 4, and 5, case 4 for data set 6, and case 5b for data sets 2 and 3. After examination of the residuals, however, it is apparent that 5b is not an appropriate solution for data sets 2 and 3. This case is approximately a step function (Fig. 4A, 4B), and the density residuals are either large on the vertical segment of the curve or nearly zero on the horizontal segments. This is not true for case 5a, where density residuals have an approximately normal distribution. If the testing sequence begins with case 5a as the alternative hypothesis, then the null hypothesis of case 1 cannot be rejected for either data set 2 or 3.

OLS parameter estimates for case 3 are identical to the EV estimates (Table 3), and estimates of p, q, and r are somewhat similar for the other cases. However, conclusions drawn from the OLS model are distinctly different. For example, case 3 cannot always be rejected on the basis of a high sum of squares; in fact, case 3 has a lower sum of squares than case 1 for four of the six data sets. On the basis of F-tests, the accepted solutions are case 1 for data sets 1 and 4, case 2 for data set 2, case 3 for data set 3, and case 4 for data sets 5 and 6. However,

TABLE 3. Parameter estimates and minimum sums of squares S for the OLS version of the model.

Data set	Case	p	q	r	min S
1. Aug QB	1	—	102	—	5.437[a]
	2	—	125	5.8	4.662
	3	1.86	—	—	59.654
	4	0.18	96	—	4.855
	5	−0.73	206	20.3	3.941
2. Aug RF	1	—	92	—	84.163
	2	—	479	95.1	30.132[a]
	3	3.07	—	—	47.058
	4	2.15	38	—	30.347
	5	0.81	323	61.7	27.821
3. Aug RF/LC	1	—	104	—	97.956
	2	—	537	100.7	34.893
	3	3.38	—	—	48.360[b]
	4	2.50	36	—	34.070[a]
	5	1.23	312	56.3	30.185
4. Sea QB	1	—	91	—	8.570[a]
	2	—	115	6.3	7.855
	3	1.66	—	—	66.948
	4	0.18	86	—	7.919
	5	0.00	116	6.5	7.623
5. Sea RF	1	—	78	—	67.074
	2	—	393	87.9	29.911
	3	2.64	—	—	48.090
	4	1.70	38	—	27.501[a]
	5	1.26	124	20.5	27.025
6. Sea RF/LC	1	—	82	—	80.489
	2	—	450	96.5	31.070
	3	2.88	—	—	46.034
	4	1.98	36	—	27.596[a]
	5	1.35	170	31.1	26.105

[a]Case selected by both F-tests and residual tests.
[b]Case selected by F-tests.

after examination of the residuals, it is apparent that case 3 is not an appropriate solution. The residuals in CPUE are mainly negative at low densities and positive at high densities (Fig. 4C). After eliminating case 3 for this reason, case 4 is the accepted solution for data set 3.

Figure 5 shows the final solutions for both the EV (solid line) and OLS models (broken line). Additional lines on the figures connect data points to the corresponding EV estimates of density and CPUE on the curve. The slopes of these connecting lines differ in accordance with the values of the weighting factors f_i and g_i for density and CPUE. In particular, notice that points with a high density d_i tend to have the greatest horizontal displacement from the curve.

Data set 1 is the best data set and there is little difference between the EV and OLS solutions. Data set 4 is similar, but with more variation in the data. In the EV model for this data set, the density value of the highest density point is reduced; consequently, the EV solution has a higher slope than the OLS solution. For data set 2, the accepted case differs between the two models. For the OLS model there is evidence of a high density effect (case 2) that is absent from the EV model (case 1). In general, this occurs because the EV model can account for a low CPUE at high density simply by assuming a large error in the density. For data sets 3 and 5, the two models again give different accepted cases, but in these data sets the OLS model indicates a low density effect (case 4) absent from the EV model (case 1). For data set 6, the accepted solution is case 4 for both the EV and the OLS models. As for data sets 1 and 4, the EV solution has a higher slope.

Differences between the EV and the OLS solutions are shown more clearly in Table 4 by the percentage significance level for each possible hypothesis test. These percentages can be interpreted in the Bayesian sense of belief or disbelief. Values in the table increase in proportion to the degree of belief in the null hypothesis. Conversely, the smaller the significance level, the greater the tendency to reject the null hypothesis in favor of the alternative hypothesis.

As an example in the use of Table 4, consider data set 3, the data set with greatest variation around the estimated curves. Figures 4C and 6 show the five possible solutions for both the EV and OLS models. Given case 1 as the null hypothesis, a significant improvement (at the 5% level) is obtained by adding one or two parameters to the OLS model, although there is less improvement with two parameters. The improvement is marginal for the EV model, and we are more likely to believe that case 1 is appropriate. The reverse situation occurs if we start with case 3 as the null hypothesis; a significant improvement is obtained by adding one or two parameters to the EV model but not to the OLS model, although (as described above) OLS case 3 can be rejected on the basis of residual analysis. For both the EV and OLS models, more improvement is obtained by adding a low density effect to case 2 than a high density effect to case 4.

As a second example, consider data set 1 (Fig. 5A), the data set with least variation around the estimated curves. Given case 3 as the null hypothesis, a significant improvement is obtained by adding one or two parameters to both the EV and OLS models. With case 1, 2, or 4 as the null hypothesis, we are more likely to add parameters to the EV than to the OLS model, and a significant improvement to the EV model is obtained by adding a low density effect to case 2.

Notice that no single case is accepted or rejected in these examples. Rather, the various possibilities are evaluated in terms of relative belief or disbelief. We find this Bayesian position more credible than the ultimate acceptance of a single case by a rigorous hypothesis testing procedure.

Discussion

In this paper we present a general model for relating a pair of stock-abundance indices, such as CPUE and observed density. The model allows five possibilities for the form of the resulting relationship. At the extremes are cases of strict proportionality (case 1) and no relationship (case 3). The other three possibilities allow for a modification of proportionality at low densities (case 4), high densities (case 2), or both (case 5). We also consider two error structures. The first (the EV model) includes error in both variables. The second (the OLS model) assumes that the density is known perfectly and that error is confined to the prediction of CPUE.

We have applied this model to data on nearshore reef fishes from the Strait of Georgia, British Columbia. We have shown that CPUE, as determined by research angling, is related to visual fish counts from a submersible. For the single-species data sets 1 and 4, the relationship appears to be one of strict proportionality. For the multispecies data sets, however, the

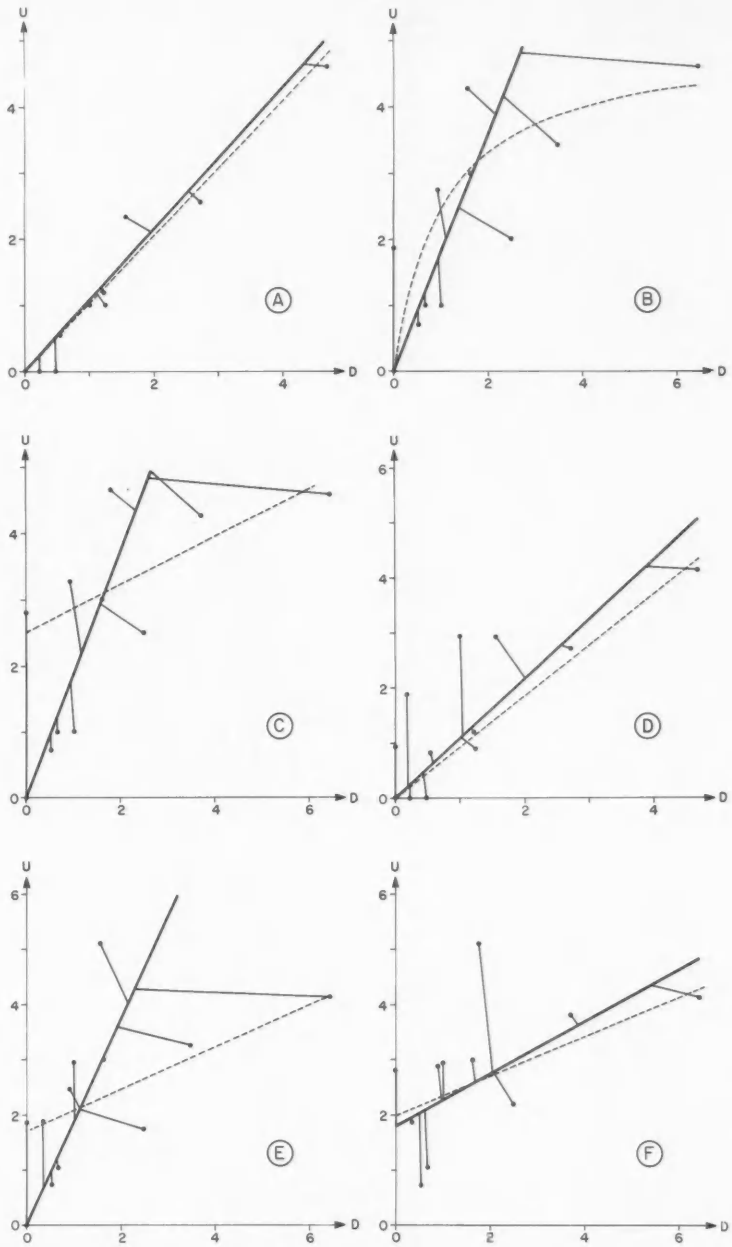


FIG. 5. Final solutions for the relationship between CPUE (U, fish·line^{-1}·h^{-1}) and the density index (D, fish·(100 m^2)$^{-1}$) for the EV model (solid line) and OLS model (broken line). The thin lines connect data points to the corresponding EV estimates of density and CPUE on the curve. (A) Data set 1, Aug QB; (B) data set 2, Aug RF; (C) data set 3, Aug RF/LC; (D) data set 4, Sea QB; (E) data set 5, Sea RF; (F) data set 6, Sea RF/LC.

shape of the relationship is somewhat ill-determined. Due to the amount of error allowed by the EV model, it is difficult to reject strict proportionality, except for data set 6 (Sea RF/LC) in which nonproportionality is indicated at low densities. By contrast, the OLS model would indicate that the relationship is sometimes asymptotic at high densities.

A key aspect of the difference between the EV and OLS models is that the EV model can explain a low CPUE at high density by allowing for error in the density measurement. Since the OLS model assumes that density is measured without error,

TABLE 4. Percentage significance levels associated with all possible hypothesis tests for the EV and OLS models. In each case the percentage corresponds to a probability, given that the null hypothesis H_0 is true, of achieving the minimum value of A (EV model) or S (OLS model) associated with the alternative hypothesis H_1. Thus a low percentage favors rejecting H_0 in favor of H_1.

EV model					OLS model			
	H_1					H_1		
H_0	2	4	5a	5b	H_0	2	4	5a
				Data set 1				
1	92.0	15.2	8.4		1	28.2	35.6	32.4
2			2.6		2			29.1
3		0.0	0.0		3		0.0	0.0
4			8.8		4			24.3
				Data set 2				
1	8.7	21.9	16.7	1.1	1	0.5	0.5	2.1
2			41.7	1.3	2			46.7
3		0.0	0.0	0.0	3		6.9	15.9
4			15.0	0.6	4			45.1
				Data set 3				
1	8.8	6.4	9.0	1.7	1	0.3	0.3	0.9
2			16.6	2.2	2			32.7
3		0.1	0.2	0.0	3		10.4	19.2
4			23.8	3.0	4			37.4
				Data set 4				
1	70.4	86.2	15.5		1	38.9	41.1	62.7
2			5.8		2			63.7
3		0.0	0.0		3		0.0	0.0
4			5.5		4			59.4
				Data set 5				
1	6.9	19.9	12.5	4.1	1	0.9	0.6	2.6
2			35.8	7.9	2			38.2
3		0.0	0.0	0.1	3		2.9	10.0
4			11.3	2.9	4			71.7
				Data set 6				
1	1.2	0.7	1.1	1.6	1	0.4	0.2	1.1
2			10.4	16.3	2			25.2
3		0.0	0.1	0.1	3		3.7	10.3
4			18.1	29.6	4			51.8

it must explain a low CPUE at high density with an asymptotic relationship. Both models exhibit some ambiguity between low and high density departures from proportionality. Thus, a non-proportional relationship (case 1 rejected) can be explained, with nearly equal credibility, by effects at either low (case 4) or high (case 2) densities.

This apparent ambiguity could, to some extent, be resolved with larger sample sizes. Our density estimates had a high variance, reflecting high habitat heterogeneity and only a few transects at each site. Unfortunately, submersible data are expensive to obtain. In our case it was necessary to trade off the number of replicate transects with the number of sites that could be visited.

It is more usual, however, to compare year-to-year changes in CPUE and abundance for one area than to compare differences among areas at one time. For one area, studied over a time period, independent data on the time dynamics of the population may be available (e.g. size–frequency data). Such data could be incorporated into an expanded model based on possible CPUE and density trends. If time trends exist, the expanded model would lead to stronger conclusions than those available from the data here.

Bannerot and Austin (1983) suggested a different approach to the problem of estimating abundance from CPUE data. They asked whether descriptors of the CPUE frequency distribution other than the mean also index abundance. They evaluated their potential candidates for a better index by correlation, using CPUE sport fishery data and corresponding abundance estimates obtained by SCUBA. For their data, the relative frequency of zero catch and its natural-log and square-root transforms had higher correlations with abundance than mean CPUE. Although their approach was ingeneous, it is still necessary to determine the appropriate form for the relationship between any new index of abundance and the chosen abundance measure.

CPUE is traditionally used in management as an index of stock abundance. The value of such an index depends both on the shape of the relationship between CPUE and abundance and on the associated level of confidence. We found the best fit to our data when we restricted the analysis to the most abundant species, the modal depth for that species, and the time interval during which weather conditions were most favorable for research angling. Athough linear relationships were predicted for species combinations and less favorable fishing conditions, the low confidence in shape of the relationship makes the predictive value less useful. Hence, the assumption of strict proportionality is best for single-species data collected over uniform weather conditions. Such data can be obtained under research conditions. CPUE has less value as an abundance index when data are combined over species and fishing conditions, as in the available commercial fishery statistics.

The management value of the relationship that we obtained for nearshore reef fishes also depends on how closely our density estimates match the density of fish susceptible to the gear. Visual counts are known to underestimate the numbers of both species and individuals in fish populations (Sale and Douglas 1981; Brock 1982). Brock (1982) compared visual estimates of fish abundance on coral reefs with collections made by rotenone. He found that visual transects underestimated abundance of the most cryptic and the highly abundant species, but "reasonably" sampled other species. Parker and Ross (1985) compared SCUBA counts with counts made by submersible at the same sites. They reported higher abundance estimates of the small and partially hidden species by SCUBA, while more of the large, less abundant species were recorded by submersible, as a larger area could be covered.

We attempted to minimize the error in our visual counts by excluding small and cryptic species, schooling species, and small rockfish from the analysis. However, we probably underestimated density in some areas due to high bottom relief. It is not possible to examine cracks and crevices in the bottom terrain unless the submersible passes directly over the crevice. Hence, fish can only be counted if they are in an exposed

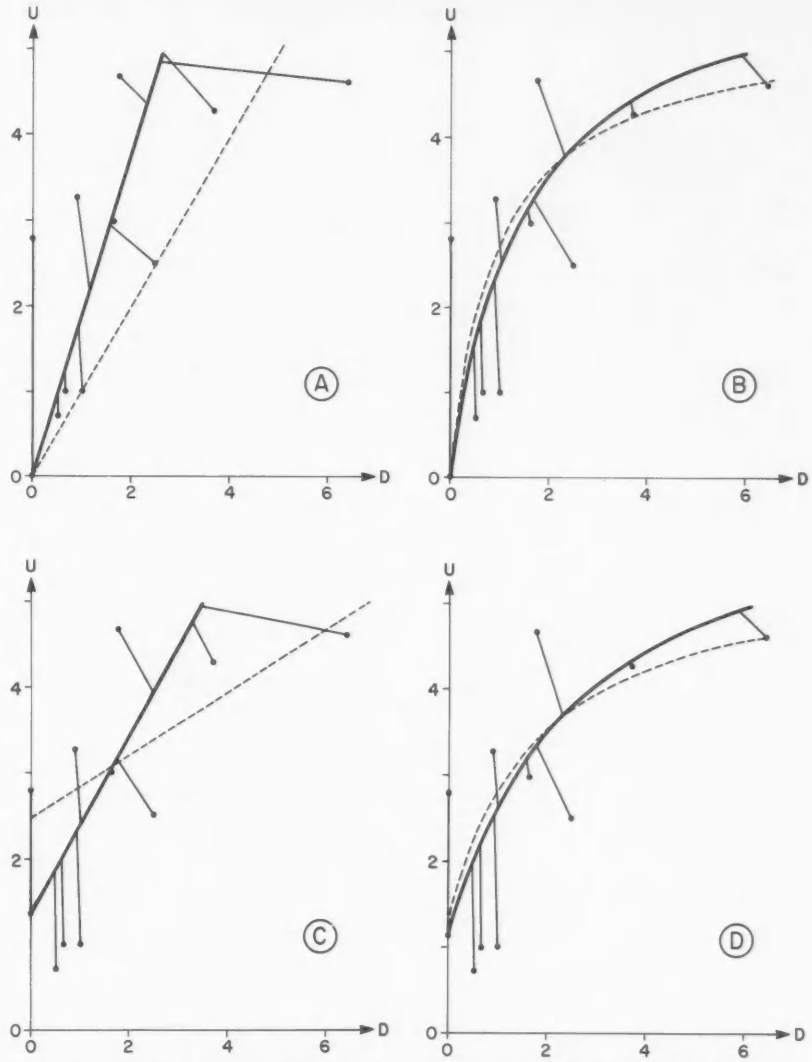


FIG. 6. Data set 3 (Aug RF/LC) solutions for the relationship between CPUE (U, fish·line^{-1}·h^{-1}) and the density index (D, fish·(100 m^2)$^{-1}$) for the EV model (solid line) and the OLS model (broken line). The thin lines connect data points to the corresponding EV estimates of density and CPUE on the curve. Case 3 is shown in Fig. 4C. (A) Case 1; (B) case 2; (C) case 4; (D) case 5a.

position, and density estimates more correctly represent estimates of minimum density.

Submersibles have been increasing in popularity as a fisheries research tool (e.g. Colin 1974; Tyler 1983; Parker and Ross 1986; Ralston et al. 1986). They are especially useful for surveys of deep-reef habitats where traditional survey methods such as bottom trawl are inappropriate (Uzmann et al. 1977; Parker and Ross 1985). Ralston et al. (1986) recently compared handline CPUE with visual density estimates from submersible observations at Johnston Atoll in the central Pacific Ocean. Although there was a positive trend in their data, they did not obtain a significant correlation between CPUE and density. Their sample size was small and they were unable to separate counts by species. By combining densities and catch across species with very different behaviors (solitary or schooling; attracted, neutral, or repelled by the submersible) and hence with very different catchabilities, they may have obscured trends in their data as we have shown here.

The species assemblage in the shallow (less than 100 m) waters of the Strait of Georgia is comparatively simple. We were able to count individual species, replicate the transect counts, dive at more sites, and estimate species size to determine whether or not they were susceptible to the gear. Our techniques would not be applicable to other *Sebastes* species such as *S. melanops* or *S. flavidus*, as these are schooling and not solitary species. These species are present in the Strait of

Georgia (Hart 1973) but they were not present in our catches or our observations.

Acknowledgements

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References

BANNEROT, S. P., AND C. B. AUSTIN. 1983. Using frequency distributions of catch per unit effort to measure fish-stock abundance. Trans. Am. Fish. Soc. 112: 608–617.

BROCK, R. E. 1982. A critique of the visual census method for assessing coral reef fish populations. Bull. Mar. Sci. 32: 269–276.

COLIN, P. L. 1974. Observation and collection of deep-reef fishes off the coasts of Jamaica and British Honduras (Belize). Mar. Biol. 24: 29–38.

GULLAND, J. A. 1964. Catch per unit effort as a measure of abundance. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 155: 8–14.

HART, J. L. 1973. Pacific fishes of Canada. Bull. Fish. Res. Board Can. 180: 740 p.

KENDALL, M. 1980. Multivariate analysis. MacMillan Publ. Co., Inc., New York, NY. 210 p.

LUDWIG, D., AND C. J. WALTERS. 1981. Measurement errors and uncertainty in parameter estimates for stock and recruitment. Can. J. Fish. Aquat. Sci. 38: 711–720.

MACKIE, G. O., AND C. E. MILLS. 1983. Use of the *Pisces IV* submersible for zooplankton studies in coastal waters of British Columbia. Can. J. Fish. Aquat. Sci. 40: 763–776.

MATHEWS, S. B., AND M. W. BARKER. 1983. Movements of rockfish (*Sebastes*) tagged in northern Puget Sound, Washington. Fish. Bull. U.S. 82: 916–922.

MITTERTREINER, A., AND J. SCHNUTE. 1985. Simplex: a manual and software package for easy nonlinear parameter estimation and interpretation in fishery research. Can. Tech. Rep. Fish. Aquat. Sci. 1384: 90 p.

NELDER, J. A., AND R. MEAD. 1965. A simplex method for function minimization. Comput. J. 7: 308–313.

O'NEILL, R. 1971. Algorithm AS 47, function minimization using a simplex procedure. Appl. Stat. 20: 338–345.

PALOHEIMO, J. E., AND L. M. DICKIE. 1964. Abundance and fishing success. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 155: 152–163.

PARKER, R. O. JR., AND S. W. ROSS. 1986. Observing reef fishes from submersibles off North Carolina. Northeast Gulf Sci. 8: 31–49.

PETERMAN, R. M., AND G. J. STEER. 1981. Relation between sport-fishing catchability coefficients and salmon abundance. Trans. Am. Fish. Soc. 110: 585–593.

RALSTON, S., R. M. GOODING, AND G. M. LUDWIG. 1986. An ecological survey and comparison of bottom fish resource assessments (submersible versus handline fishing) at Johnston Atoll. Fish. Bull. U.S. 84. (In press)

RICHARDS, L. J., AND A. J. CASS. 1985. Transect counts of rockfish in the Strait of Georgia from the submersible *Pisces IV*, October & November 1984. Can. Data Rep. Fish. Aquat. Sci. 511: 99 p.

RICHARDS, L. J., A. J. CASS, J. R. SELSBY, R. VAN DEN BROEK, AND S. D. LOYNACHAN. 1985. A summary of research catch and effort data for nearshore reef-fishes collected during 1984 in MSA 15 and 16 of the Strait of Georgia. Can. MS Rep. Fish. Aquat. Sci. 1833: 69 p.

RICKER, W. E. 1940. Relation of "catch per unit effort" to abundance and rate of exploitation. J. Fish. Res. Board Can. 5: 43–70.

1944. Further notes on fishing mortality and effort. Copeia 1944: 23–44.

ROTHSCHILD, B. J. 1977. Fishing effort, p 96–115. *In* J. A. Gulland [ed.] Fish population dynamics. John Wiley & Sons Ltd., Toronto, Ont. 372 p.

SALE, P. F., AND W. A. DOUGLAS. 1981. Precision and accuracy of visual census techniques for fish assemblages on coral patch reefs. Environ. Biol. Fishes 6: 333–339.

SCHNUTE, J. 1984. Linear mixtures: a new approach to bivariate trend lines. J. Am. Stat. Assoc. 79: 1–8.

TYLER, W. A. III. 1983. Population estimates of commercially important reef fishes using mark/recapture and visual census techniques on the Florida middle grounds. M.Sc. thesis, University of South Alabama, Mobile, AL. 94 p.

UHLER, R. 1980. Least squares regression estimates of the Schaefer production model: some Monte Carlo simulation results. Can. J. Fish. Aquat. Sci. 37: 1284–1294.

UZMANN, J. R., R. A. COOPER, R. B. THEROUX, AND R. L. WIGLEY. 1977. Synoptic comparison of three sampling techniques for estimating abundance and distribution of selected megafauna: submersible vs camera sled vs otter trawl. Mar. Fish. Rev. 39: 11–19.

WALTERS, C. J., AND D. LUDWIG. 1981. Effects of measurement errors on the assessment of stock–recruitment relationships. Can. J. Fish. Aquat. Sci. 38: 704–710.

Appendix: Data Compilation and Calculation of λ

This appendix describes the methods used to compile the raw data and to determine estimates for the variance weights (f_i, g_i) in (5) and (6) and the variance ratio λ in (7). We exploit the fact that replicate transects were conducted by *Pisces IV* at most sites and research angling times were generally divided into more than one period.

To estimate the variance in density, first let d_{ij} $(i=1,\ldots,k;$ $j=1,\ldots,m_i)$ represent the observed density on the jth transect at the ith site, with the total number of transects

$$m = \sum_{i=1}^{k} m_i.$$

Then, following (5), assume that

$$d_{ij} = d_i + \alpha f_i \delta_{ij} \quad \text{(A.1)}$$

where d_i is the mean and αf_i is the standard deviation of d_{ij} and δ_{ij} is a normal random variable with mean 0 and variance 1. We explored two possibilities for the weighting factors f_i:

$$f_i = 1, \quad \text{(A.2)}$$

that is, standard deviation independent of site, and

$$f_i = d_i, \quad \text{(A.3)}$$

that is, standard deviation proportional to site density. In both cases, site density is estimated as the mean:

$$\hat{d}_i = (1/m_i) \sum_{j=1}^{m_i} d_{ij}. \quad \text{(A.4)}$$

After examination of residual plots for all species combinations, we chose (A.3) as more representative of the density data. Thus, from (A.3) and (A.4) we obtain estimates of $\hat{d}_i$ and $\hat{f}_i$ to be used in the model. Furthermore, α^2 can be estimated from a sum of squares of residuals:

$$\hat{\alpha}^2 = \frac{1}{m-k} \sum_{i=1}^{k} \sum_{j=1}^{m_i} [(d_{ij} - \hat{d}_i)/\hat{f}_i]^2 \quad \text{(A.5)}$$

where the correction factor $1/(m-k)$ allows for the fact that k df are lost due to estimating d_i for $i = 1,\ldots,k$. Notice that αf_i in (A.1) is the standard deviation of a single observation d_{ij}. This is not the same as the standard deviation in observed density $\hat{d}_i$, because $\hat{d}_i$ is the mean of m_i observations. The average number of observations per site is m/k so that an estimate for σ^2 in model equation (5) is

$$\hat{\sigma}^2 = (k/m)\hat{\alpha}^2. \quad \text{(A.6)}$$

These calculations are at best approximate and are designed only to give estimates of the variance weights required by the EV model. Transects could not always be replicated, and the mean density at some sites was 0. The above calculations apply only to sites with at least two transects and a nonzero mean. The assumption (A.3) is a convenient way to estimate the variance at sites with only one transect. Furthermore, at sites

with 0 mean ($\hat{d}_i = 0$), we assume that

(A.7) $f_i = 0.001$ fish·m^{-2}

since this approximates the lowest visually measurable density.

To estimate the variance in CPUE, let u_{ij} ($i = 1,\ldots,k$; $j = 1,\ldots,n_i$) represent the observed CPUE from the jth time period at the ith site. We again explored two possibilities, namely

(A.8) $u_{ij} = u_i + \beta\epsilon_{ij}$

(A.9) $u_{ij} = u_i + (\beta/e_{ij})\epsilon_{ij}$

where β is a standard deviation, e_{ij} is the effort associated with u_{ij}, and ϵ_{ij} is a standard normal random variable. In (A.8) the standard deviation is independent of the site, while in (A.9) it is inversely proportional to the associated effort. The estimate for u_i in (A.8) is the usual mean:

(A.10) $\hat{u}_i = (1/n_i)\sum_{j=1}^{n_i} u_{ij}$

while the estimate for u_i based on (A.9) is a mean weighted by e_{ij}:

(A.11) $\hat{u}_i = \left[\sum_{j=1}^{n_i} (e_{ij}u_{ij})\right] \Big/ \left[\sum_{j=1}^{n_i} e_{ij}\right].$

Thus, if c_i and e_i represent the total catch and effort, respectively, at site i, the estimate $\hat{u}_i$ based on (A.9) is simply the ratio

(A.12) $\hat{u}_i = c_i/e_i.$

There was little difference between assumptions (A.8) and (A.9) indicated by residual plots of the CPUE data. We chose (A.9) as more reasonable, as we had more confidence in catches associated with longer fishing times. Analogous to (A.5), the estimate for β^2 in (A.9) is

(A.13) $\hat{\beta}^2 = \frac{1}{n-k}\sum_{i=1}^{k}\sum_{j=1}^{n_i}[e_{ij}(u_{ij}-\hat{u}_i)]^2$

where n is the sum of the n_i, that is, the total number of fishing periods.

It can be shown from (A.9) that $\hat{u}_i$ in (A.12) has standard deviation $\beta/(e_i n_i)$, where the factor n_i occurs because $\hat{u}_i$ is the weighted mean of n_i observations. As with the density measurements, we approximate n_i by the average number n/k of observations per site. Then (A.9) is consistent with model equation (6), subject to the three conditions: that u_i is taken from (A.12), that τ is estimated by

(A.14) $\hat{\tau}^2 = (k/n)\hat{\beta}^2,$

and that the weighting factor g_i is taken to be

(A.15) $g_i = 1/e_i.$

Comparisons of Herring Otoliths Using Fourier Series Shape Analysis

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Numeric analysis of otolith morphology provides vital information to commercial fisheries concerning the age distribution, racial origin, and, to some extent, the environmental history of fish stocks. Conventional methods used to retrieve these data, though proven to be effective, are time consuming, susceptible to ambiguous interpretations, and only semiquantitative. Fourier shape descriptors, when used to analyze outlines of otolith silhouettes, represent a rapid, objective, semiautomated means of obtaining much of this information. Analysis of Fourier shape information derived from otoliths of juvenile and adult Alaskan herring and adult Northwest Atlantic herring show that otolith shape reflects differences in fish age and fish race. The shape of otoliths of juvenile fish are significantly different from those of adult fish. Few shape differences can be found, though, between otoliths from adult fish of different age within the same stock. Distinct differences exist between Atlantic and Alaskan adult otolith shapes. For some stocks, minor shape differences occur between left and right otoliths. Differences in otolith shape arising from sexual dimorphism are not apparent.

L'analyse numérique de la morphologie des otolithes fournit des informations essentielles pour les pêches commerciales au sujet de la répartition des âges, de l'origine raciale et, jusqu'à un certain point, de l'histoire environnementale des stocks de poisson. Les méthodes classiques utilisées pour obtenir ces données, bien qu'elles s'avèrent efficaces, exigent beaucoup de temps, peuvent prêter à des interprétations ambiguës et ne sont que semi-quantitatives. Les descripteurs de forme par série de Fourier, lorsqu'ils sont utilisés pour analyser le contour des otolithes, représentent un moyen rapide, objectif et semi-automatisé permettant d'obtenir une bonne partie de cette information. L'analyse des données sur la forme par série de Fourier obtenues à partir d'otolithes de harengs jeunes et adultes de l'Alaska et de harengs adultes de l'Atlantique nord-ouest montre que la forme des otolithes traduit les différences observées dans l'âge et la race des poissons. La forme des otolithes de jeunes poissons est sensiblement différente de celle des poissons adultes. Cependant, on peut observer quelques différences de forme entre les otolithes de poissons adultes d'âges différents faisant partie du même stock. Il y a des différences nettes entre la forme des otolithes de harengs adultes de l'Alaska et de l'Atlantique. Pour certains stocks, il y a de petites différences dans la forme entre les otolithes droites et gauches. Il n'y a pas de différences apparentes dans la forme des otolithes en raison du dimorphisme sexuel.

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Otoliths provide important information for the scientific management of commercial fisheries. Age, racial origin, and, to an extent, environmental history may be determined from the number and spacing of growth rings in, and morphology of, an otolith (Einarsson 1951; Blacker 1974; Postuma 1974; Messieh 1975; Rowell 1980). Several investigators have shown that analysis of otolith morphology is useful for determining the composition of herring stocks. Einarsson (1951), Zijlstra (1958), and Postuma (1974) emphasized the importance of both size and shape of the otolith nucleus, while Parrish and Sharman (1958) emphasized "growth zones" of the otolith. Messieh (1972, 1975) demonstrated that angular relationships between readily recognizable features of otolith shapes were useful for differentiating between individuals of spring and fall spawning populations of Northwest Atlantic herring.

Microscopic examination of otoliths is the normal method of obtaining this information, but it is time consuming, susceptible to ambiguous interpretations, and semiquantitative at best. This approach, though useful for major classification of groups, is not powerful enough to differentiate between regional subgroups. Semiautomated shape analysis tehniques offer improvements in speed and ease over more traditional techniques. The method described in this paper, Fourier series analysis of otolith outlines, results in mathematical descriptions

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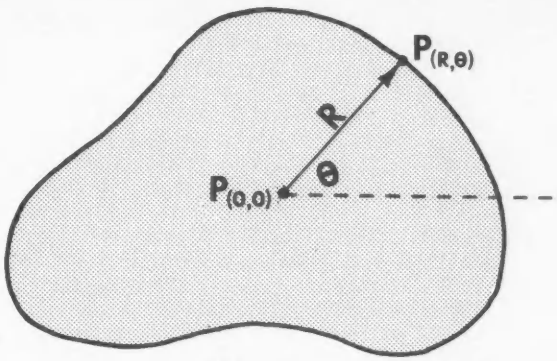

$$R(\theta) = A_o + \sum_{n=1}^{\infty} A_n \cos(n\theta - \phi_n)$$

FIG. 1. Computation of the Fourier series based on radii drawn from the shape centroid to a Nyquist set of points on the shape periphery.

of a silhouette that can be used both to describe and to compare otolith shapes quantitatively. Fourier shape analysis is not only capable of making these differentiations, but because of its geometric approach, we speculate that it may provide insights into events that influence otolith growth, such as insufficient nutrition during maturation.

Fourier Series Shape Analysis

Fourier shape descriptors, called harmonics, are generated by taking a Fourier expansion of radius vectors drawn from the centroid of a shape as a function of angle about the centroid (Fig. 1). The length of the radius R at angle θ is given by

$$(1) \quad R(\theta) = A_0 + \sum_{n=1}^{\infty} A_n \cos(n\theta - \phi_n)$$

where θ is the polar angle measured from an arbitrary reference point, A_0 is the mean radius of the shape (the amplitude of the 0th harmonic), A_n is the amplitude of the nth harmonic, and ϕ_n is the phase angle of the nth harmonic (Ehrlich and Weinberg 1970). Any shape that can be described as a single-valued function about a centroid can be analyzed according to this method. A single-valued function occurs when each radius passes through only one point on the object's outline.

The Fourier series as applied in this study is calculated for the maximum projected shape of each otolith using coordinates of a Nyquist set of points sampled around the shape periphery. The number of points sampled for each shape is at least twice the number of harmonics that will be computed, which is 24. Points are sampled at equal angular intervals using the shape centroid as origin. The centroid of the shape and the Nyquist set of coordinates are determined iteratively from the digitized shape outline using methods described by Full and Ehrlich (1982). Although a valid Fourier series can be calculated with the origin at any location, choice of the centroid as origin allows comparisons between otoliths.

When the centroid is selected as the origin, each harmonic amplitude (A_n) represents the relative contribution to the empiric shape of a characteristic shape component (harmonic) (Fig. 2). The amplitude of the second harmonic, for example, represents the contribution of a figure-eight to the empiric shape and is a measure of elongation (Fig. 3). The third harmonic is a trefoil and measures triangularity. The fourth represents the contribution of a quadrefoil and measures squareness. In general, the "nth" harmonic represents the contribution of an "n-leaved clover." Amplitudes measure the relative dominance of each harmonic and phase angles measure the orientation of each harmonic with respect to an arbitrary reference. The observed shape thus is partitioned into a series of terms where gross shape (elongation, triangularity, and so forth) is measured by harmonics of low order (generally less than 8). Increasingly fine-scale surface sculpture is measured at higher orders (Fig. 3).

Fourier analysis, given enough terms, captures all the information required to describe shape completely. As a consequence, two-dimensional shape can be described quantitatively to whatever degree of precision is required by using a Fourier series. This can be demonstrated by computing the Fourier series of amplitudes and phase angles for a given shape and then using only the information contained in the Fourier series to reconstruct the shape. If information is either missed or lost in the process, the original shape will not be reconstructed accurately. Comparison of the original shape (stippled, Fig. 4) with the final reconstructed shape (21), formed by successive additions of the first 20 terms in the Fourier series, shows that they are virtually identical. Note that the gross shape of otoliths is determined largely by the first six harmonics and that addition of successively higher order harmonics adds increasingly finer detail to the shape.

Strategies for analyzing Fourier shape data that employ standard statistical and multivariate methods have been developed by Ehrlich et al. (1980), Hudson (1979), Gevirtz (1976), and Full et al. (1981, 1982). Analytic techniques normally operate on the distribution of amplitudes that characterize a given sample rather than the phase angles. These techniques include chi-square analysis of contingency tables (Maxwell 1971), R- and Q-mode factor analysis (Klovan and Miesch 1976; Miesch 1976; Full et al. 1981, 1982; Eppler et al. 1983), and fuzzy set analysis applied to k-means and c-means clustering (Bezdek 1980; Bezdek et al. 1984) (Fig. 5). The principal method of analysis used for the study reported here is chi-square contingency table analysis.

The chi-square technique makes comparisons between aggregate shape characteristics displayed by entire samples of shapes. A single sample consists of n shapes, each of which is described by 24 harmonics. Shape characteristics of each sample, then, are contained in a $24 \times n$ matrix of harmonic amplitudes. Each column of the array contains 24 amplitudes that describe a specific shape in the sample. Each row of the array contains n amplitudes that describe shape variation displayed by the sample within a given harmonic. Shape differences that exist between samples are identified by making orthogonal comparisons between respective rows of data that represent different samples. Specifically, maximum entropy histograms (Full et al. 1984) are constructed that show the pattern and range of variation in amplitudes (A_n's, Eq. 1) within each harmonic (row). Significant differences between these harmonics are detected by making a chi-square test between distributions formed within each harmonic according to methods described by Maxwell (1971).

Methods

Otoliths from juvenile and adult herring from Alaska and

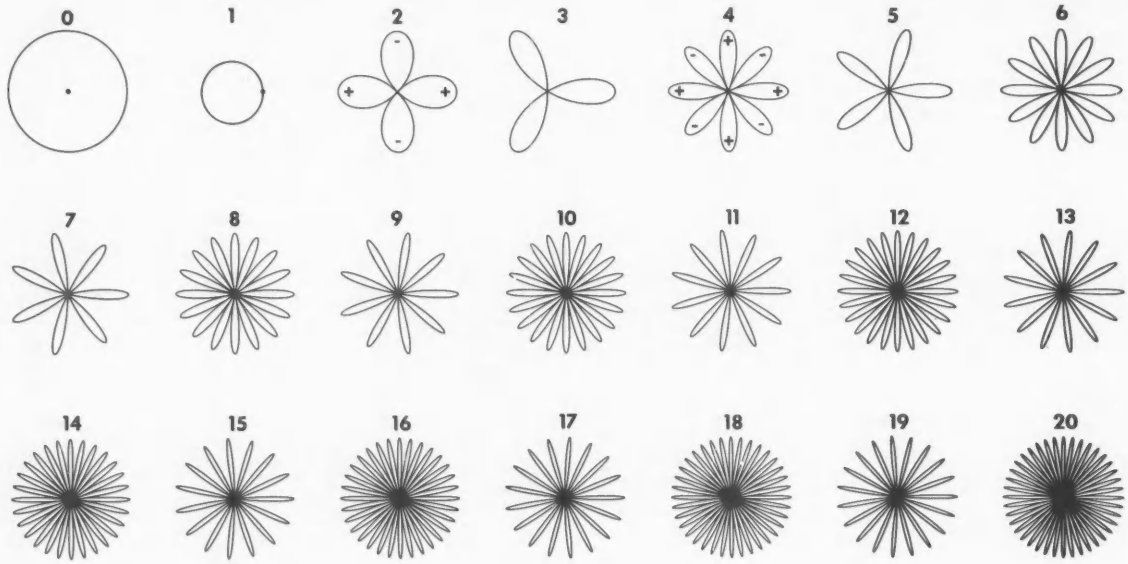

FIG. 2. Graphic representation of selected harmonics. Plus and minus signs on even-numbered harmonics indicate that alternating lobes are subtracted when shape components are summed. Amplitude = 1.0 and phase angle = 0 for all harmonics.

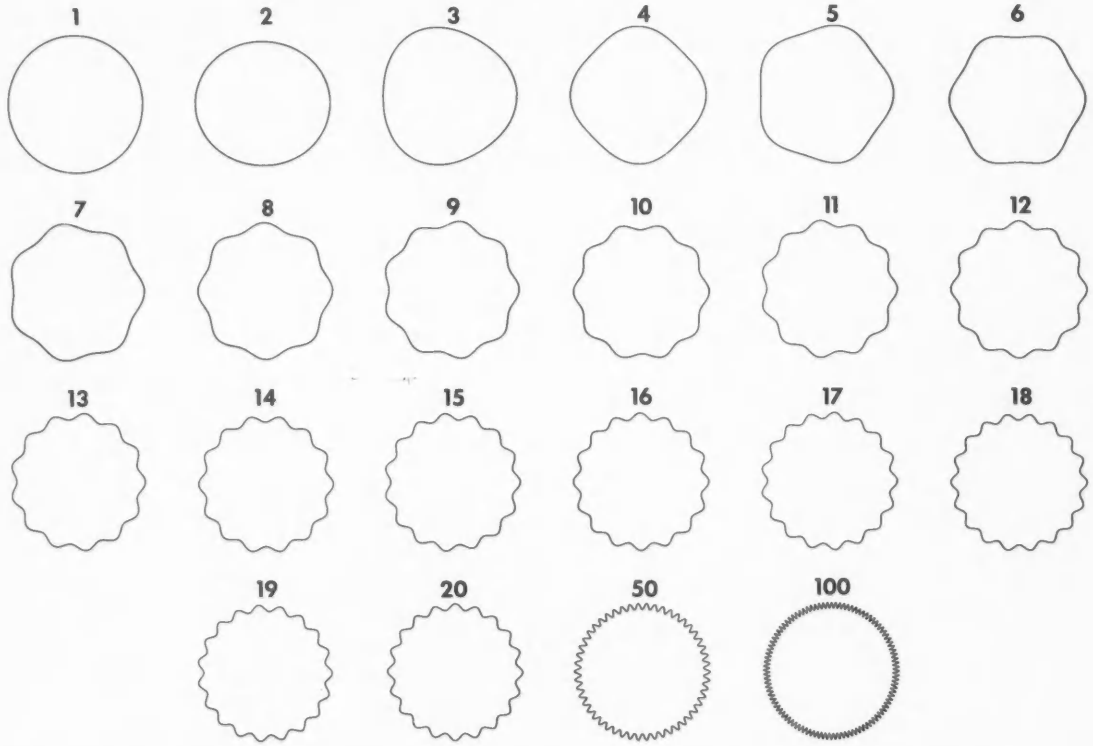

FIG. 3. Imprint of selected harmonics (Fig. 2) on a circle (zeroth harmonic). Note that the number of lobes produced by any given shape component is the same as the harmonic number. Low-order harmonics (2−6) modify gross shape. Higher-order harmonics produce increasingly fine-scale perturbations in shape. Amplitude of the zeroth harmonic is 1.00; that of all the others is 0.02. Phase angles of all harmonics is 0.

TABLE 1. Chi-square comparisons between selected groups of otoliths based on physiological, regional, and age differences.

Comparison	Significant harmonics (95% level)	Sample size
Bilateral symmetry, juveniles	None	152
Bilateral symmetry, adults	5, 11, 15, 18	415
Sexual dimorphism	None	408
Fish length (200–275 mm, 25 mm classes)	17, 18	415
Fish weight (100–400 g, 50 g classes)	6, 11, 13, 15, 20, 21	411
Otolith diameter (A_0, Eq. 1)	2, 4–9, 11–15, 21–23	75
Regional Comparisons		
Alaska, Norton Sound vs. Togiak, all adults	6, 9, 20	414
Alaska, Norton Sound vs. Togiak, 5-yr-olds	2, 3, 6, 24	195
Atlantic vs. Alaska, all adults	3, 5–7, 15–17, 19, 21–23	631
Georges Bank vs. Norton Sound	2, 3, 5, 6, 8–11, 13, 14, 16–23	414
Georges Bank vs. Gulf of St. Lawrence, 5-yr-olds	3, 5–6, 7, 14, 16	160
Gulf of St. Lawrence vs. Norton Sound, 5-yr-olds	2, 3, 5, 7, 8, 10, 11	170
Age Comparisons		
Norton Sound 5- vs. 6-yr-olds	14, 16, 17, 24	257
Georges Bank 5- vs. 6-yr-olds	14, 15, 17, 20	91
Gulf of St. Lawrence, 1975 vs. 1977 vs. 1978 catches (5-yr-olds)	3, 5, 7	69
Gulf of St. Lawrence, Spring vs. fall spawners	3, 4, 8, 10, 11, 17	69

adult herring from the Northwest Atlantic comprise the sample sets examined in this study. Video images of otoliths from juvenile herring from Alaska were obtained for digitizing from drawings made with the aid of a dissecting microscope and a camera lucida. Images of otoliths from adult fish from Alaska were obtained through a stereomicroscope using transmitted light. Images of otoliths from adult fish from the Atlantic were obtained through a stereomicroscope using two sources of reflected light. The shape analysis system (Fig. 5) obtained a video image from a TV camera, either through a microscope or regular TV lens. The image was digitized and pixels on otolith outlines were identified using algorithms developed by Fico (1980). Coodinates of these pixels were passed to the Fourier analysis program which then generated a harmonic series for each sample (Ehrlich and Full 1983).

Next, each sample set was subdivided on the basis of fish length, weight, otolith radius, sampling locale, and age. An objective measure of otolith radius was obtained from the Fourier series computed for each otolith (A_0, Eq. 1). Fish age was determined by counts of otolith rings in the case of the juvenile Alaskan herring, or provided as part of the data accompanying the other otolith samples. These groupings were compared for significant differences in the frequency distribution of amplitudes for all harmonics (Table 1).

Results and Discussion

Slight modifications were made to a generalized otolith shape (Fig. 6) to examine the sensitivity of Fourier analysis to slight differences in shape. The modifications were based on the nature of shape variation observed in otolith samples. Modified shapes were compared with unmodified shapes (Table 2), but no statistical examination of these results was conducted. Because the modifications are qualitative, the observed variation patterns are more important than the actual values of the changes of harmonic amplitudes between shape 1 and the other shapes in Fig. 6. Any ranking scheme for these results is unrealistic, since the modifications were arbitrary. Table 2 shows which harmonics increased or decreased due to the modifications. It must be remembered that other modifications in degree and kind could have easily altered these patterns.

Shape 2 differed from shape 1 by having an elongated rostrum (Fig. 6). This change had the greatest effect of all modifications (Table 2) based on increases in harmonic amplitudes. The next most influential modification was shape 8 in which the width of the rostrum was trimmed. Both modifications resulted in an increase in most harmonic amplitudes. Shapes that increase the length to width ratio and create a more elongated shape show more increases than decreases in amplitude. Shapes that tend to decrease this ratio show fewer increases than decreases in amplitude.

Results of the chi-square comparisons of groupings (Table 1) made on physiological rather than a population basis are not surprising. No significant variations were observed between the right and left otoliths of juvenile herring from Alaska. Some variations were noted for adult herring from Alaska, and these were found mainly in the middle-level harmonics (Table 1), suggesting that differences occurred in outline roughness and not in gross shape characteristics. This variation could be due either to a difference in the growth rates of right or left otoliths or to the result of abnormal growth (Schoen and Von Holst 1950, cited in Blacker 1974). There were no discernible differences attributable to sexual dimorphism.

The only differences related to the length of adult fish are in high-order harmonics which measure surface roughness. This is surprising because several authors observe that there is a linear relationship between otolith length and fish length (Watson 1964; Messieh 1975). We demonstrate above that slight changes in otolith length-to-height ratios produce marked changes in amplitudes of both low-order and high-order harmonics. Fourier shape descriptors, then, should be sensitive indicators of changes in otolith length. It is possible that increases in otolith size in adults are relatively uniform, and that changes in otolith shape are very slight after maturity is

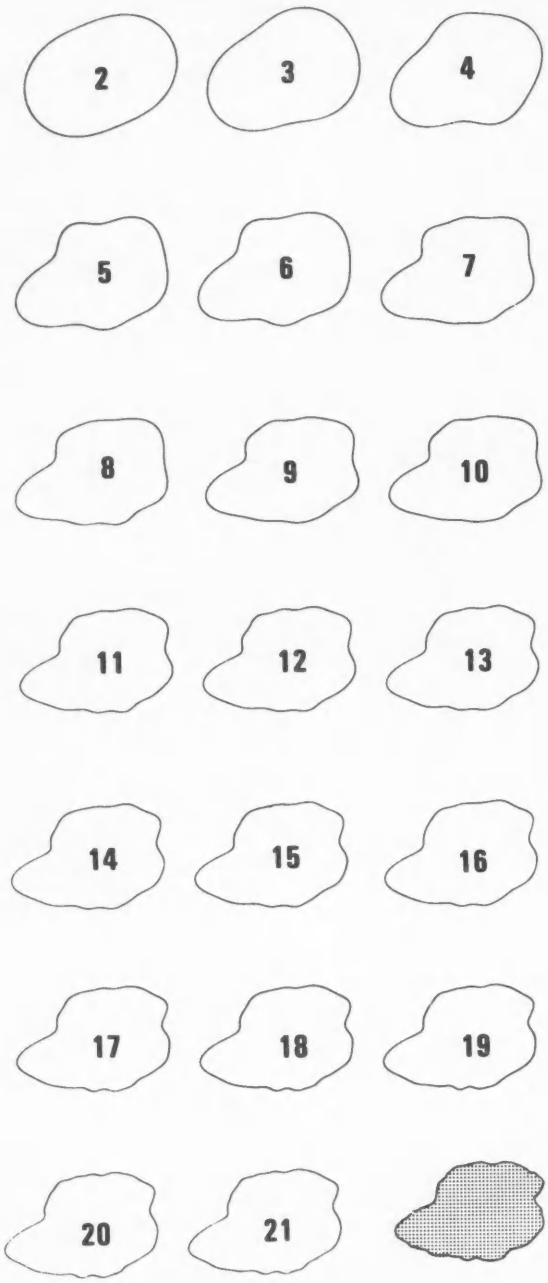

FIG. 4. Shape reproduction by addition of Fourier shape components (harmonics). Fourier harmonics were computed for the stippled shape shown. The first 20 harmonics were summed in sequence using Eq. 1 (see text). After each harmonic was added, the resultant shape was plotted. Thus, shape 5 represents the sum total of shape information contained in the first five harmonics, shape 10 the information in the first 10 harmonics, and so on. The high degree of similarilty that exists between the original shape and shape 21 indicates that nearly all information concerning shape is captured in the Fourier series.

TABLE 2. Harmonics that increased in amplitude in response to shape changes shown in Fig. 6.

Modification No.	Harmonic No.
1	(Original shape)
2	1–22, 24
3	2, 4, 6, 8, 10, 12–19
4	1, 2, 13–22, 24
5	2, 3, 5, 8, 10, 12, 14, 15, 18, 20, 22
6	1–4, 12, 14, 16, 18, 20–22
7	1, 2, 4, 6, 8, 10, 12–15, 17–21
8	1, 3, 5–24
9	4, 6–8, 10–12, 14–16, 18, 19, 22, 24

reached. If so, this would contrast with the development pattern of juvenile herring in which there is a definite change in otolith shape with growth (Messieh 1975). Comparisons of juvenile otoliths grouped by otolith diameter were highly variable, and variations in 15 harmonics were significant (Table 1). This variation is interesting, but because of growth patterns and small sample size, we could not determine whether the differences between otoliths were due to age or racial differences.

Regional subgroups as a class demonstrated the most variation of any of our comparisons. Considerable differences were seen in the comparison of Atlantic and Alaska adult herring otoliths. This difference is even more apparent when the comparison is restricted to adult herring from George's Bank of the Northwest Atlantic and adult herring of Norton Sound of Alaska. Some of the variation may be due to the confounding effects of age. This is evident when the same comparison is made on the 5-yr-old age class. When regional comparisons are made on a single age class, there are fewer significant variations. These variations are found mainly in the lower harmonics, which indicates differences in overall shape. This difference strongly supports the potential use of shape analysis to distinguish between races of fish.

When the effects of age are compared for both Atlantic and Alaska herring, significant variations occur in the mid- and higher-level harmonics. This suggests that otolith shape becomes rougher with increasing age. Comparisons of 5-yr-old herring from spring and fall breeding stocks from the Gulf of St. Lawrence showed considerable variation in the lower-level harmonics. This variation was expected, as Atlantic herring spring and fall spawning stocks are known to have otoliths that differ from each other in the shape of the post- and pararostrums (Messieh 1972). A comparison of 5-yr-old spring spawners from the same region, but caught in different years, had significant variation in fewer harmonics and only in the lower odd harmonics. This variation would indicate that a detectable difference may occur between year classes, but these variations are slight and the degree of independence of each harmonic is not clear.

Conclusion

The analysis of otolith shape as described in this paper provides a technique capable of detecting differences between samples. Further research is needed to separate the effects of individual, population, racial, and species variation. Grant (1980) and Rowell (1980) were able to differentiate between stocks of herring from the Bering Sea on the basis of biochem-

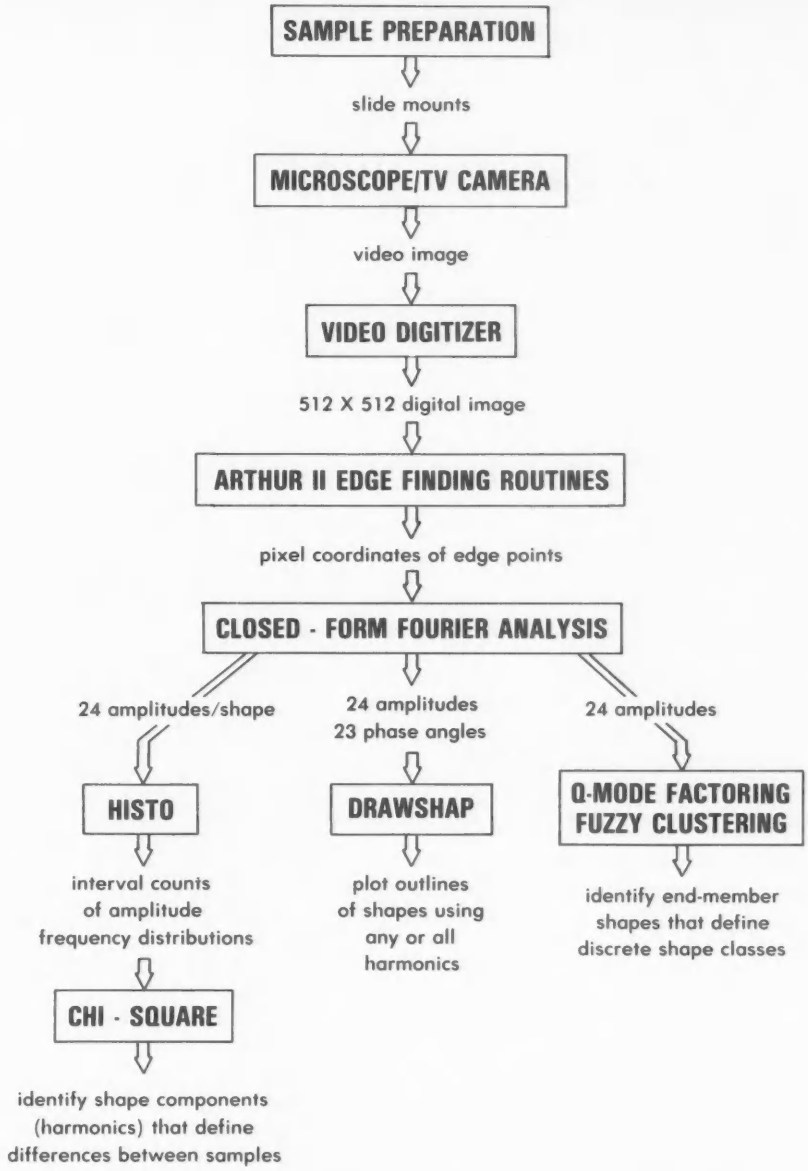

FIG. 5. Scheme for analysis of Fourier shape data. Analysis used here is confined to use of chi-square and DRAWSHAP procedures.

istry and scale morphology, respectively. Messieh (1975) differentiated between stocks of Atlantic herring based on otolith morphology. We obtain similar results on the basis of otolith shape. We detect distinct differences among Northwest Atlantic herring stocks. Differences between Alaska herring are less dramatic but are still significant between regions.

The potential usefulness of Fourier shape analysis as a fisheries management tool extends beyond the scope of our results. One major advantage of shape analysis techniques is the capability of rapidly examining large samples accurately. The shape of 100 prepared specimens can be digitized and corresponding Fourier series can be computed in less than 2 h. Computer and image processing equipment required to perform the analysis can be obtained for less than $15 000. Further research is needed to investigate such promising areas as the determination of environmental history, otolith growth patterns, phenotypic expression, and racial classification of individuals. This technique shows promise as a powerful aid in determining the origin of individuals composing a stock, an outcome that promotes more knowledgeable decisions by fisheries.

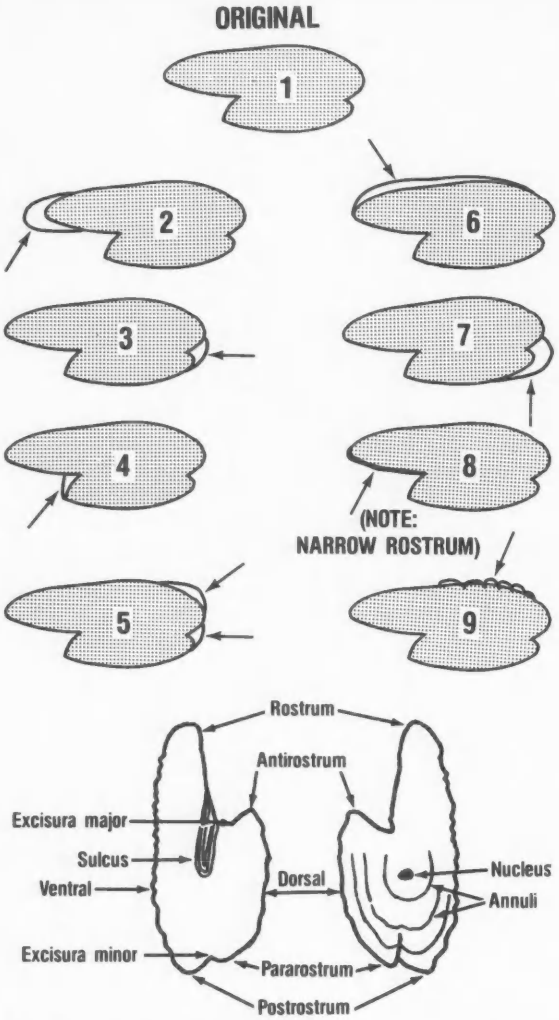

FIG. 6. Modifications to the basic shape of a herring otolith (shape 1) were made to test the sensitivity of Fourier series shape analysis to minor differences in shape. The modification involved slight changes (indicated by arrows) to shape 1. These modifications were arbitrary, but based on differences observed in otolith samples.

Acknowledgments

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References

BEZDEK, J. C. 1980. Particle and grain shape analysis with fuzzy sets, p. 121–140. *In* J. K. Beddow and T. P. Meloy [ed.] Advanced particulate morphology. CRC Press, Inc., Boca Raton, FL.

BEZDEK, J. C., R. EHRLICH, AND W. FULL. 1984. FCM: the fuzzy *c*-means clustering algorithm. Comput. Geosci. 10: 191–203.

BLACKER, R. W. 1974. Recent advances in otolith studies, p. 67–90. *In* F. R. Harden-Jones [ed.] Sea fisheries research. John Wiley & Sons, New York, NY.

EHRLICH, R., P. J. BROWN, J. M. YARUS, AND D. T. EPPLER. 1980. Analysis of particle morphology data, p. 101–119. *In* J. K. Beddow and T. P. Meloy [ed.] Advanced particulate morphology. CRC Press, Inc., Boca Raton, FL.

EHRLICH, R., AND W. E. FULL. 1983. Fourier shape analysis: a multivariate pattern recognition approach, p. 47–67. *In* R. M. Brown [ed.] NORDA Technical Note 176.

EHRLICH, R., AND B. WEINBERG. 1970. An exact method for characterization of grain shape. J. Sediment. Petrol. 40: 205–212.

EINARSSON, H. 1951. Racial analyses of Icelandic herrings by means of otoliths. Rapp. Cons. Explor. Mer 128: 55–74.

EPPLER, D. T., R. EHRLICH, D. NUMMEDAL, AND P. H. SHULTZ. 1983. Sources of shape variation in lunar impact craters: Fourier shape analysis. Geol. Soc. Am. Bull. 94: 274–291.

FICO, C. 1980. Automated particle shape analysis — development of a microprocessor controlled image analysis system. Masters thesis, University of South Carolina, Columbia, SC.

FULL, W. E., AND R. EHRLICH. 1982. Some approaches for location of centroids of quartz grain outlines to increase homology between Fourier amplitude spectra. Math. Geol. 14: 43–55.

FULL, W. E., R. EHRLICH, AND J. C. BEZDEK. 1982. FUZZY QMODEL — a new approach for linear unmixing. Math. Geol. 14: 259–270.

FULL, W. E., R. EHRLICH, AND S. K. KENNEDY. 1984. Optimal configuration and information content of sets of frequency distributions. J. Sediment. Petrol. 54: 117–126.

FULL, W. E., R. EHRLICH, AND J. E. KLOVAN. 1981. EXTENDED QMODEL — objective definition of external end members in the analysis of mixtures. Math. Geol. 13: 331–344.

GEVIRTZ, J. L. 1976. Fourier analysis of bivalve outlines: implications on evolution and autoecology. J. Int. Assoc. Math. Geol. 8: 151–163.

GRANT, S. 1980. Biochemical genetic variation in North Pacific herring, p. 261. *In* B. R. Melteff and V. G. Wespestad [ed.] Proceedings of the Alaska Herring Symposium. Alaska Sea Grant Rep. 80-4.

HUDSON, C. B. 1979. Determination of relative provenance contribution in sand samples using Q-mode factor analysis of Fourier grain shape data. M.S. thesis, University of South Carolina, Columbia, SC.

KLOVAN, J. E., AND A. T. MIESCH. 1976. EXTENDED CABFAC and QMODEL computer programs for Q-mode factor analysis of compositional data. Comput. Geosci. 1: 161–178.

MAXWELL, A. E. 1971. Analysing qualitative data. Chapman and Hall, London. 163 p.

MESSIEH, S. N. 1972. Use of otoliths in identifying herring stocks in the southern Gulf of St. Lawrence and adjacent waters. J. Fish. Res. Board Can. 29: 1113–1118.

1975. Growth of otoliths in young herring in the Bay of Fundy. Trans. Am. Fish. Soc. 104: 770–772.

MIESCH, A. T. 1976. Q-mode factor analysis of geochemical and petrologic data matrices with constant row-sums. U.S. Geol. Surv. Prof. Pap. 574-G: 47 p.

PARRISH, B. B., AND D. P. SHARMAN. 1958. Some remarks on methods used in herring "racial" investigations, with special references to otolith studies. Rapp. Cons. Explor. Mer 143: 66–80.

POSTUMA, K. H. 1974. The nucleus of the herring otolith as a racial character. J. Cons. Int. Explor. Mer 35: 121–129.

ROWELL, K. A. 1980. Separation of spawning stocks of Bering Sea herring based on scale growth patterns, p. 262–263. *In* B. R. Melteff and V. G. Wespestad [ed.] Proceedings of the Alaska Herring Symposium. Alaska Sea Grant Rep. 80-4.

SCHOEN, L., AND E. VON HOLST. 1950. Das zussamensoiel von lagena and utriculus bei der lageorientierung der knochenfische. Z. Vergl. Physiol. 32: 552–571.

WATSON, J. E. 1964. Determining the age of young herring from their otoliths. Trans. Am. Fish. Soc. 93: 11–20.

ZIJLSTRA, J. J. 1958. On herring "races" spawning in the southern North Sea and English Channel. Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer 143: 134–145.

Microhabitat–Preference Curves of Blackfly Larvae (Diptera: Simuliidae): A Comparison of Three Estimation Methods

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Three analytical techniques are available to describe the observed response of stream-dwelling organisms to variations in their physicochemical environment: the incremental method, polynomial regression on a single factor, and multiple regression. The efficacy of these tools as descriptors of the responses has not been compared. We used the three methods to describe density and microhabitat–preference curves for *Prosimulium mixtum/fuscum*, *Stegopterna mutata*, and *Simulium aureum* in response to distance from the lake, current velocity, and water depth in a stream draining a Laurentian lake. The incremental method yielded the least precise estimates of density and biased estimates of optimal current velocity for two of the three species; multiple regression yielded the most precise estimates of density and unbiased estimates of optimal conditions, whereas polynomial regression on a single factor was intermediate. From this comparison, we suggest that the multiple-regression approach to estimate microhabitat–preference curves be used in developing optimal management stategies. Further, we suggest that rare species should be excluded from such analysis because of the low precision of density estimates for rare organisms.

Trois techniques d'analyse sont disponibles pour décrire la réaction qu'on observe chez les organismes qui habitent les cours d'eau face aux variations de leur milieu physico-chimique : la méthode des charges croissantes, la régression polynomiale à un seul facteur et la régression multiple. On n'a pas comparé l'efficacité de ces outils comme descripteurs des réactions. Nous avons utilisé les trois méthodes afin de décrire les courbes de densité et de préférence en matière de microhabitat pour *Prosimulium mixtum/fuscum*, *Stegopterna mutata* et *Simulium aureum* en réponse à la distance par rapport au lac, à la vitesse du courant et à la profondeur de l'eau dans un cours d'eau qui draine un lac de la région laurentienne. La méthode des charges croissantes a donné les estimations les moins précises de la densité et des estimations faussées de la vitesse optimale du courant pour deux des trois espèces; la régression multiple a donné les estimations les plus précises de la densité et des estimations non faussées des conditions optimales tandis que la régresson polynomiale à un seul facteur a donné des résultats intermédiaires. À partir de cette comparaison, nous proposons d'utiliser l'approche de la régression multiple pour estimer les courbes de préférence en matière de microhabitat lors de l'élaboration des stratégies de gestion optimale. En outre, nous estimons qu'il faut exclure les espèces rares de ce type d'analyse en raison de la précision peu élevée des estimations de la densité pour ce qui est des organismes rares.

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Flow allocations in regulated streams and stream modifications to improve sport-fishery production should maximize the proportion of the stream suiting the preferences of desired organisms and their prey (Bovee et al. 1978; Bovee and Cochnauer 1977; Gore and Judy 1981). Both the Habitat Evaluation Procedure (U.S. Fish and Wildlife Service 1980, 1981) and the Instream Flow Incremental Method (Stalnaker 1979) use preference curves of the target species to determine habitat suitability for a sport fishery at various discharge levels. Similar analyses have been made for stream macroinvertebrates (Gore and Judy 1981; Orth and Maughan 1983).

Three different methods have been used to fit preference curves (Gore and Judy 1981; Orth and Maughan 1983). The incremental methodology (Gore and Judy 1981) is applied by first ranking the data in increasing value of some habitat variable such as velocity or depth. For each of these variables, the cumulative mean number of animals per unit increment in habitat variable is plotted as a function of that variable. If a polynomial is fitted by ordinary least squares to this cumulative

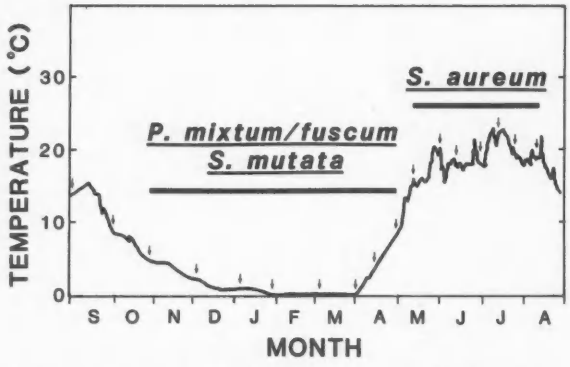

FIG. 1. Temperature regime (mean daily temperatures between September 1981 and August 1982) of the stream and sampling design of the study. Arrows indicate the sampling dates, and horizontal bars indicate the range of sampling dates at which the species were collected.

curve, the first derivative of the polynomial describes a curve peaking at the preferred velocity or depth. These curves are standardized by dividing the derivative curve by the peak derivative over the range of sampled values. This yields a preference curve for each factor, with preference values ranging between 0 and 1. The combined effect of the two variables on density is calculated as the joint preference factor, the product of the individual preference factors for velocity and depth. In polynomial regression on a single factor (Orth and Maughan 1983), the observed density in all samples is first log-transformed to stabilize variance. Independent polynomial regression models relating density to each variable are then fitted to the data. The polynomial regression is converted to a preference function by backtransforming the regression equation to arithmetic units and dividing by the maximum observed abundance. The joint preference factor is again calculated as the product of the preference factors for each variable. The multiple-regression approach (Gore and Judy 1981) describes log-transformed density as a linear or polynomial function of all habitat variables. The effect of any variable can be isolated by holding the other variables constant, and the preference curve for any variable is calculated by dividing this partial regression equation by the maximum abundance over the range of sampled values.

Ideally, preference curves should yield unbiased and precise estimates of the relative abundances of the target organisms. Lack of bias is desirable, since biased estimates of the optima for the target species would lead to suboptimal management strategies. High precision is needed to quantify precisely the benefits of a given management strategy. In this paper, we compare the accuracy and precision of models fitted by the three methods used by Gore and Judy (1981) and Orth and Maughan (1983) to determine which method yields the most accurate preference curves and the most precise estimates of density. To compare the three methods over a range of situations, we use data on three species of blackfly larvae that differ widely in density: *Prosimulium mixtum/fuscum*, *Stegopterna mutata*, and *Simulium aureum*.

Methods

This study was conducted on a second-order stream in the Lower Laurentians (Quebec) at the Station de biologie de l'Université de Montréal (46°00′N, 74°00′W). The stream flows from Lake Quatre (area 2 ha, maximum depth 2.5 m) which is formed by a beaver dam. The lake is generally ice covered from mid-November to the beginning of May; its water is acidic (pH 5.8–6.4), soft (conductivity 12–41 $\mu S \cdot cm^{-1}$), and brown (color up to 80 Pt units). The discharge varies between 80 and 1000 $L \cdot s^{-1}$ during the year. The substrate is composed of boulders (diameter 20–150 cm) partially covered with mosses. The mean depth varied between 6 and 25 cm in 1981–82.

Water temperature was measured with a minimum–maximum thermometer placed 80 m downstream from the lake. Temperature data were taken daily from May to August in 1982 and at least once a month over the rest of the sampling period. The thermal regime of the stream (Fig. 1) does not vary much from year to year (P.–P. Harper, unpubl. data) except in early summer.

Larval preference was estimated from the number of larvae that colonized ceramic tiles (500 cm^2) distributed randomly in the stream section. On September 2, 1981, 20 tiles were put in the first 50 m of the stream. These tiles were collected and replaced once a month until April 2, 1982, and then every 2 wk until May 11, 1982. On that date, 55 tiles were randomly placed in the stream section and replaced twice a month until August 15, 1982. Collected tiles were put in plastic bags and the samples preserved in the field with 4% formaldehyde. For each sample, we recorded the distance from the lake, the water depth, and the mean current velocity measured 2.5 cm above the tile with a pigmy current meter. In the laboratory, the samples were seived (75 μm), sorted, and preserved in 95% ethanol for later identification. Winter samples that contained too many larvae to be identified in a reasonable amount of time were subsampled with a Folsom plankton splitter. At least 150 individuals were counted for all subsamples. The densities estimated by subsampling correlated well with the densities observed in full samples ($r^2 = 0.93$, $n = 27$). The samples from May 11, 1982, contained early instars of several species that could not be identified accurately and this date was excluded from the analysis.

Statistical Methods

We used only the data from sampling dates at which 20 or more individuals of the species had been collected. Since several of the remaining samples contained no larvae, we first added 1 to all density estimates before logarithmic transformation. Polynomial terms were included in the regression models only when they were significant (sequential F-test, Montgomery and Peck 1982).

Lack of bias in the preference curves is reflected by the absence of trend in the residual variability. An unbiased model yields residuals which are uncorrelated with the factors included in the analyses. To detect bias in the preference curves, first we regressed the logarithms of the observed densities against the logarithms of the joint preference factor calculated by the incremental methodology, against the logarithms of the joint preference factor calculated by polynomial regression on a single factor, and against the logarithms of the values predicted from the multiple-regression model. The residuals of these models were then regressed against distance, velocity, and depth. Preference curves are considered biased when the partial regression coefficients between the residuals and distance, velocity, or depth differ significantly from 0.

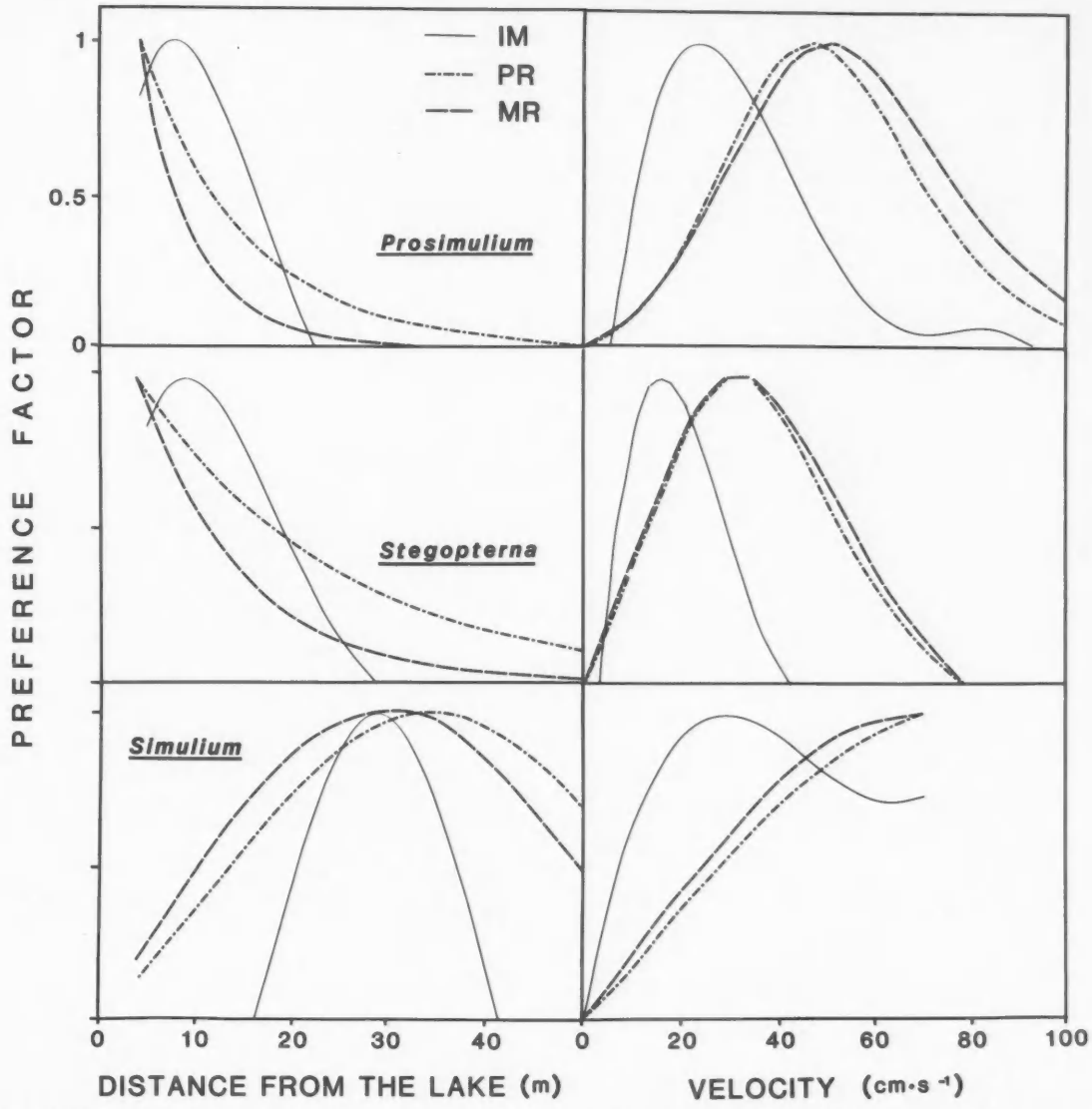

FIG. 2. Distance–preference and velocity–preference curves obtained by the incremental method (IM), the polynomial regression on a single factor (PR), and the multiple regression (MR).

The precision of the three models obtained for each species is reflected by the magnitude of the residual variability. The most precise model yields the smallest residual mean square. To quantify the precision of the three models, the logarithm of the observed density was regressed against the logarithm of the joint preference factor calculated by the incremental methodology, the logarithm of the joint preference factor calculated by polynomial regression on a single factor, and the logarithm of the predicted values of the multiple-regression model. The significance of the differences in precision of the three models was determined by calculating the ratio of the residual mean square errors of the two models to be compared. This ratio was compared with critical values of F with $n - 2$ degrees of freedom for both numerator and denominator, where n is the number of samples used in the analysis.

Results and Discussion

The three species were not equally abundant in the studied section. Over 63 000 larvae of *Prosimulium mixtum/fuscum* were collected in 155 samples retained for the analysis, an average of 413 individuals per tile (SD = 922). *Stegopterna mutata* was the second most abundant species, with 709 individuals in 98 samples retained, averaging 7.2 individuals per tile (SD = 12.05). *Simulium aureum* was rarer; only 248 individuals were collected in 199 samples, an average of 1.25 individuals per tile (SD = 3.55).

The distance–preference and velocity–preference curves

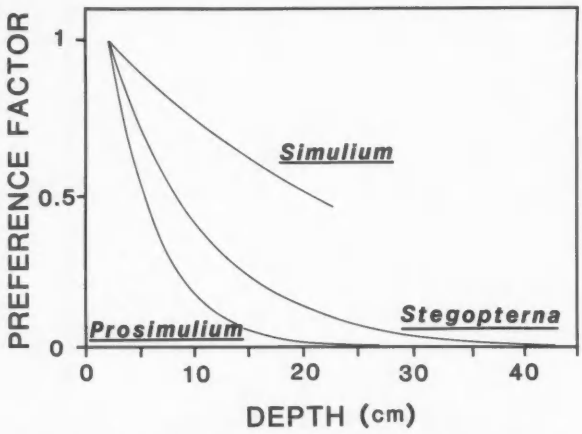

FIG. 3. Depth–preference curve obtained by the multiple-regression method for *Prosimulium mixtum/fuscum*, *Stegopterna mutata*, and *Simulium aureum*. The preference curves obtained by the two other methods were almost identical and coincided with the curves obtained by the multiple regression.

obtained with the three methods are illustrated in Fig. 2. Since the depth–preference curves obtained with the three methods are almost identical and coincide on the graph, only the depth–preference curves obtained by multiple regression are shown in Fig. 3. The general shape of the preference curves obtained with the three methods is similar for all three factors.

The relative density of *Prosimulium mixtum/fuscum* and of *Stegopterna mutata* decreased exponentially with increasing distance from the lake, whereas the abundance of *Simulium aureum* was maximal 30–35 m from the lake and then decreased downstream. The abundances of filter-feeders generally decrease downstream from lakes (Hynes 1970), and the overwintering larvae of *Prosimulium mixtum/fuscum* and *Stegopterna mutata* followed this general trend. However, *Simulium aureum*, which inhabited the stream in summer, did not. The first 30 m of the studied section also supports dense populations of Hydropsychidae (mainly *Cheumatopsyche pettiti* and *Hydropsyche betteni*), which are relatively inactive during the winter but grow rapidly in early summer (Morin and Harper 1986). Hydropsychids can dislodge blackfly larvae (Hemphill and Cooper 1983) and may contribute to the absence of *Simulium aureum* in the presumably best sites immediately downstream from the lake (Carlsson et al. 1977). The rate of downstream decrease of *Prosimulium mixtum/fuscum* ($6.9\% \cdot m^{-1}$, multiple-regression estimate) is close to the estimate of Sheldon and Oswood (1977) for all simuliids in the outlet of Placid Lake, Montana ($8.2\% \cdot m^{-1}$ immediately below the lake), but is much higher than the downstream decrease of *Prosimulium* spp. in the outlet of Lake Stukeley ($0.45\% \cdot m^{-1}$) and Lake Orford ($0.12\% \cdot m^{-1}$) in southern Quebec (A. Morin, unpubl. data). The rate of downstream decrease in density varies from stream to stream, and these differences might relate to differences in the rate of downstream decline of seston quality or quantity.

The three species responded differently to current velocity (Fig. 2). *Prosimulium mixtum/fuscum* preferred faster currents than *Stegopterna mutata*. *Simulium aureum* prefers fast current but shows a wider preferendum than the two other species. Because the current meter was held 2.5 cm from the bottom,

TABLE 1. Accuracy of the preference curves for distance, velocity, and depth estimated by the incremental method (IM), polynomial regression on a single factor (PR), and the multiple regression (MR). Listed values are the probabilities that the partial regression coefficients between the residuals and distance, velocity, or depth are equal to 0, i.e. that the preference curve is unbiased (NS > 0.05). These indications of bias were confirmed by nonparametric analysis for trend and scrutiny of the residuals.

Factor	IM	PR	MR
Prosimulium mixtum/fuscum			
Distance	0.0002	NS	NS
Velocity	0.0001	NS	NS
Depth	NS	NS	NS
Stegopterna mutata			
Distance	0.0004	0.0013	NS
Velocity	0.0006	NS	NS
Depth	NS	NS	NS
Simulium aureum			
Distance	0.0067	NS	NS
Velocity	NS	NS	NS
Depth	NS	NS	NS

the optimal current velocities identified by the preference curves are well above the velocities actually experienced by the larvae. Since slow microcurrents can be found even in fast-flowing riffles, blackfly species that prefer slow current could occur at low or high velocities, and would have a relatively flat velocity–preference curve. *Simulium aureum*, which is morphologically adapted to slow current, exhibits such a preference curve. *Stegopterna mutata* is also adapted to slow currents; however, its preference curve drops more rapidly above the optimal velocity. The presence of *Prosimulium mixtum/fuscum* at high velocities might contribute to this rapid decline, since both inhabit the stream in winter. The tiles in optimal conditions for *Prosimulium* were thick with larvae, and it is possible that *Prosimulium* out-competed *Stegopterna* on these tiles.

The density of the three species decreased exponentially with increasing depth (Fig. 3), even though the depth ranged only between 3 and 44 cm. It seems unlikely that differences in pressure, oxygen concentration, or light would explain the preference of blackflies for shallow water. The effect of depth might reflect turbulence (Statzner 1981; Orth and Maughan 1983), which depends on velocity and depth. Larvae in shallower water may also profit more from the surface film which is rich in lipids (Wotton 1982).

Bias in the Preference Curves

The shape of the preference curves calculated by the incremental method differed from those obtained by the two other methods, as did the positions of the optima. Analysis of residuals of the three models revealed that the distance–preference curves obtained with the incremental method were biased for all three species (Table 1). In addition, the incremental method yielded biased velocity–preference curves for *Prosimulium mixtum/fuscum* and *Stegopterna mutata*. Polynomial regression on a single factor usually yielded preference curves similar to the unbiased preference curves obtained with multiple regression, but underestimated the rate of downstream decrease of *Stegopterna* density.

TABLE 2. Comparison of the precision of the density estimates obtained by the incremental method (IM), the polynomial regression on a single factor (PR), and the multiple regression (MR). n = number of samples; R^2 = coefficient of determination; RMS = residual mean square; F = ratio of RMS of the model to RMS of the "best" model; P = probability that the precision of the model is equal to the precision of the "best" model. The conclusions of these tests were confirmed by non-parametric analysis for differences in central tendancy. All regressions were highly significant (F-test, $p < 0.0001$).

Method	R^2	RMS	F	p
Prosimulium mixtum/fuscum (n = 155)				
IM	0.41	0.689	1.606	0.002
PR	0.55	0.534	1.245	0.088
MR	0.64	0.429		
Stegopterna mutata (n = 98)				
IM	0.20	0.244	1.554	0.016
PR	0.23	0.236	1.503	0.023
MR	0.49	0.157		
Simulium aureum (n = 199)				
IM	0.20	0.083	1.012	0.467
PR	0.16	0.088	1.073	0.311
MR	0.22	0.082		

Examination of the residuals to the models revealed that the data did not entirely satisfy the assumptions of normality and homoscedasticity (see Fig. 4). Consequently, nonparametric analysis of the residuals was also performed (Spearman's rank correlation). The results of these analyses confirmed the bias detected by parametric analysis.

Multiple regression was the only approach that yielded unbiased preference curves for the three species, and should therefore be preferred to the two other methods. Orth and Maughan (1983) argued that polynomial regression on a single factor could be used to derive preference curves with fewer data points than would be required to derive multivariate preference functions, since fewer coefficients have to be estimated simultaneously. This study suggests that polynomial regression on a single factor yields unbiased preference curves; however, this would not be the case if a synergism strongly influences abundance (Gore and Judy 1981) or if some of the predictor variables are correlated. Multicollinearity will introduce bias in the preference functions when the factors are considered independently (as in incremental method and in polynomial regression on a single factor), but its effect on the preference functions derived with the multiple regression is to increase the standard error of the estimates of the regression coefficients (Montgomery and Peck 1982). The resulting preference curves would then identify less precisely the optimum conditions but would not be systematically biased. In principle, multicollinearity may be avoided by collecting a "balanced" data set, one that represents all combinations of factors equally. Since strong correlations exist between some habitat variables (velocity, substrate, depth, and periphyton for example), it might be difficult to collect a perfectly balanced data set in practice. Multiple regression should therefore be preferred to the two other methods.

Precision

The multiple-regression model was significantly more precise than the models fitted by incremental methodology and polynomial regression on a single factor for *Prosimulium mixtum/fuscum* and *Stegopterna mutata*. The three models yielded similar precision for *Simulium aureum* (Table 2). A nonparametric test of the precision of the three models was also performed (Wilcoxon rank-sum statistic). The results of this analysis confirmed the parametric analysis.

In Fig. 4, the observed densities of the three species are plotted against the predicted values by multiple regression, with approximate 95% confidence intervals of the predictions for the mean and the individual values. The plots for *Simulium aureum* and *Stegopterna mutata* show that the data points at low observed density are not distributed normally around the one-to-one line. This can be attributed to the samples with no larvae. Since the densities are expressed per tile (500 cm^2) and each point represents one tile, it is impossible to measure densities below 1 individual per 500 cm^2. Low densities cannot be measured unless large sampling devices are used, or several samples are pooled. Preference curves derived for rare species are imprecise, and the utility of such preference curves in stream management is questionable. The sampling cost of precise abundance estimates of rare species is prohibitive (Morin 1985) so that, until rapid and cheap sampling and processing methods are available, rare species should be ignored in quantitative studies.

The models illustrated in Fig. 4 provide estimates of expected density in a variety of conditions. Observed densities lie within an order of magnitude of the predicted density. The residual variability could be due to natural variability among replicate samples, to variability among sampling dates, to other variables that influence density, and to variability in the predictor variables. The predictor variables were measured at the time of collection but the density of larvae on the tiles probably reflects conditions during the entire colonization period. Continuous monitoring of the predictor variables could probably reduce the scatter around the predictions of the model, but such an approach would dramatically increase the logistic costs. The scatter around the predicted values in Fig. 4 is probably partially due to the coarseness of the measurements of the independent variables, and may eventually be reduced with improvements of the monitoring techniques. The multiple-regression approach is flexible enough to include more factors and remove

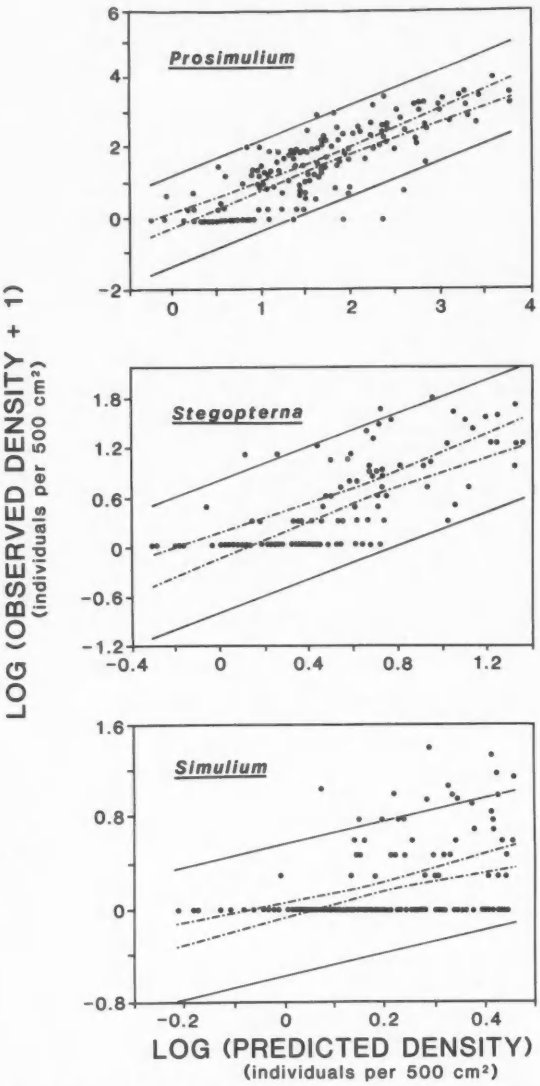

FIG. 4. Comparison of the observed densities with those predicted by the multiple-regression models, with approximate 95% confidence belts for the mean (broken lines) and for individual predicted values (solid lines). Multiple-regression models for the three species: $\log_{10}$ (density of *Prosimulium* + 1) = $3.21 - 0.079d + 0.070v - 0.00092v^2 + 0.0000026v^3 - 0.095z$; $\log_{10}$ (density of *Stegopterna* + 1) = $1.34 - 0.042d + 0.042v - 0.00086v^2 + 0.0000042v^3 - 0.049z$; $\log_{10}$ (density of *Simulium* + 1) = $-0.027 + 0.016d - 0.00027d^2 + 0.0087v - 0.000064v^2 - 0.016z$; where d is the distance from the lake (m), v is the current velocity ($cm \cdot s^{-1}$), and z is the water depth (cm).

some of these potential sources of error. Among the supplementary factors that could account for some differences among "replicates" are density of predators and of competitors, periphyton biomass and structure, colonization time, and sampling date.

The models presented here assume that preferences observed on tiles reflect the preferences of the larvae rather than the rate of colonization of the tiles. This assumption is supported by the similarity of the preference curves derived from simultaneous observations on artificial and natural substrates (A. Morin, unpubl. data).

A recent critique of the Instream Flow Incremental Methodology (Mathur et al. 1985) questions the validity of the approach, since observed abundances are weakly correlated with predictions. The critique is relevant although it fails to consider low precision and bias of the preference curves as a possible explanation for the observed low correlations. The preference curves and the hydraulic model are the two basic components of the Instream Flow Incremental Methodology, and the full method cannot yield more precise predictions than the predictions from the preference curves or the hydraulic model. Unfortunately, published preference curves do not include estimates of errors of the predictions; it is therefore impossible to determine whether the low correlations between potential available habitat (WUA) and fish biomass show that the method fails to describe response to changes in WUA, or only that the model is so imprecise that it yields predictions of low value.

All published models (Gore and Judy 1981; Orth and Maughan 1983; this study) have been developed from data collected from single streams. Before published preference curves are used to manage several streams, more information should be obtained about the generality of these curves. For example, we must know if they are accurate in different streams or in different years.

Considering the lack of bias of the preference curves, the higher precision of the predictions, and the future possibility that other factors may be considered, we suggest that the multiple regression is the most useful approach in the estimation of preference curves. Such analysis should, however, be restricted to abundant species, since the presence of many samples with zero density decreases the precision of estimated preference curves.

Acknowledgments

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References

BOVEE, K. D., AND T. COCHNAUER. 1977. Development and evaluation of weighted criteria, probability-of-use curves for instream flow assessments: fisheries. Instream Flow Info. Pap. No. 3, U.S. Fish and Wildlife Service, FWS/OBS-77/63: 53 p.

BOVEE, K. D., J. A. GORE, AND A. J. SILVERMAN. 1978. Field testing and adaptation of a methodology to measure "in-stream" values in the Tongue River, Northern Great Plains (NGP) region. U.S. Environ. Prot. Agency, EPA-908/4-78–004A: 465 p.

CARLSSON, M. L., L. M. NILSSON, B. J. SVENSSON, S. ULFSTRAND, AND R. S. WOTTON. 1977. Lacustrine seston and other factors influencing the blackflies (Diptera: Simuliidae) inhabiting lake outlets in Swedish Lapland. Oikos 29: 379–396.

GORE, J. A., AND R. D. JUDY JR. 1981. Predictive models of benthic macroinvertebrate density for use in instream flow studies and regulated flow management. Can. J. Fish. Aquat. Sci. 38: 1363–1370.

HEMPHILL, N., AND S. D. COOPER. 1983. The effect of physical disturbance on the relative abundances of two filter-feeding insects in a small stream.

Oecologia (Berl.) 58: 378–382.
HYNES, H. B. N. 1970. The ecology of running waters. University of Toronto Press, Downsview, Ont. 555 p.
MATHUR, D., W. H. BASON, E. J. PURDY, JR., AND C. A. SILVER. 1985. A critique of the Instream Flow Incremental Methodology. Can. J. Fish. Aquat. Sci. 42: 825–831.
MONTGOMERY, D. C., AND E. A. PECK. 1982. Introduction to linear regression analysis. John Wiley & Sons, New York, NY. 473 p.
MORIN A. 1985. Variability of density estimates and the optimization of sampling programs for stream benthos. Can. J. Fish. Aquat. Sci. 42: 1530–1534.
MORIN, A., AND P.-P. HARPER. 1986. Phénologie et microdistribution des adultes et des larves de Trichoptères filtreurs dans un ruisseau des Basses Laurentides. Arch. Hydrobiol. (In press)
ORTH, D. J., AND O. E. MAUGHAN. 1983. Microhabitat preferences of benthic fauna in a woodland stream. Hydrobiologia 106: 157–168.
SHELDON, A. L., AND M. W. OSWOOD. 1977. Blackfly abundance in a lake outlet: test of a predictive model. Hydrobiologia 56: 113–120.
STALNAKER, C. B. 1979. The use of habitat structure preferenda for establishing flow regimes necessary for maintenance of fish habitat. *In* J. V. Ward and J. A. Stanford [ed.]. The ecology of regulated streams. Plenum Press, New York, NY, 398 p.
STATZNER, B. 1981. A method to estimate the population size of benthic macroinvertebrates in streams. Oecologia (Berl.) 51: 157–161.
U.S. FISH AND WILDLIFE SERVICE. 1980. Habitat evaluation procedures (HEP). Division of Ecological Services, ESM 102, Washington, DC. 84 p.
1981. Standards for the development of habitat suitability index models. Division of Ecological Services, ESM 103, Washington, DC. 113 p.
WOTTON, R. S. 1982. Does the surface film of lakes provide a source of food for animals living in lake outlets? Limnol. Oceanogr. 27: 959–960.

Variation in Male Parr Maturation Within and Among Populations of Atlantic Salmon, *Salmo salar*

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The covariation of growth and maturation in male Atlantic salmon parr, *Salmo salar*, produces a relationship characterized by a size threshold below which individuals generally do not mature. The threshold of 70–72 mm fork length is evident both within and among populations. Parr maturation can reduce growth during the second year of life by an average of 4.0%. Among-year variation in growth rate affects the yearly incidence of maturation for males at age 1+ but has no detectable effect on the total proportion of male parr maturing in a population. Increases in the proportion of mature parr in the Matamek River, Quebec, can be explained by variation in growth alone; there is no evidence for genetic changes in this population.

La covariation de la croissance et de la maturation chez les tacons de saumon de l'Atlantique, *Salmo salar*, produit une relation caractérisée par un seuil de taille au-dessous duquel les mâles n'atteignent généralement pas la maturité. Un seuil variant de 70 à 72 mm de longueur à la fourche est évident au sein de populations et entre celles-ci. La maturation des tacons peut réduire la croissance par une moyen de 4 % de la deuxième année du cycle vital. La variation du taux de croissance d'une année à l'autre influe sur la fréquence annuelle de la maturation des mâles à 1+ an, mais n'a aucune incidence discernable sur la proportion totale de tacons mâles d'une population que atteignent la maturité. La variation de la croissance peut, à elle seule, expliquer les augmentations de la proportion de tacons matures présents dans la rivière Matamek (Québec); il n'ya aucune evidence de changements genitiques dans cette population.

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The sexual maturation of male Atlantic salmon parr, *Salmo salar*, is a common phenomenon throughout the geographical range of this species, occurring at varying levels of incidence among populations (Jones 1959; Schiefer 1971; Dalley et al. 1983). This early maturation can have profound demographic consequences on salmon populations (Saunders and Schom 1985). High mortality and delayed smoltification associated with parr maturation reduces male salmon production by 60% in Newfoundland (Myers 1984). There is evidence from laboratory (Alm 1959; Leyzerovich 1973; Saunders et al. 1982; Thorpe et al. 1983) and field (Schiefer 1971; Dalley et al. 1983) research that males destined to mature as parr initially have a faster mean growth rate than male parr that do not mature before migration to sea. Although studies on hatchery Atlantic salmon have shown that maturing parr grow faster at first (Murphy 1980) and then at a slower rate than immature parr after the commencement of gonadal development, i.e. in the late summer and autumn before spawning (Leyzerovich 1973; Saunders et al. 1982), there has been no attempt to quantify this effect for naturally occurring populations.

The purpose of this study is to collate and analyze systematically all available data on parr maturation among North American populations of Atlantic salmon to determine the degree to which growth and maturation covary within and among natural populations. It is necessary to have this information to determine whether differences in such maturation among populations, and changes within populations over time, can be attributed to variation in growth rate alone.

Furthermore, we wish to determine whether between-year variation in growth affects the proportion of a cohort that matures as parr. Although yearly variations may affect the age at maturation, there are no data to indicate whether yearly changes in growth affect the total proportion of males that mature as parr over the lifetime of a cohort. This information is important to the theoretical development of stock–recruitment relationships for Atlantic salmon because of the high mortality associated with parr maturation.

Our objectives in this paper are fourfold. First, we estimate the reduction in growth associated with maturation of male

TABLE 1. Heterogeneity factors computed for Little Codroy River and Miramichi River.

	Sites	$\bar{n}$	α	β	ϵ	Heterogeneity factor
Little Codroy						
57	11	6.4	56.90	20.10	0.013	1.1
58	10	8.4	4.10	1.43	0.180	2.1
59	14	4.8	5.96	3.80	0.091	1.4
60	31	11.0	2.17	0.77	0.340	3.5
61	22	4.8	0.30	0.32	1.610	5.2
62	23	6.7	5.50	1.74	0.140	1.7
63	27	7.4	4.90	1.90	0.150	1.8
Total	138	7.9	1.82	0.84	0.380	2.9
Miramichi	14	12	0.60	1.09	0.59	5.2

parr. Second, we compare patterns of growth and parr maturation among and within populations. Third, we determine whether significant differences exist in the incidence of mature male parr among populations, once growth effects have been statistically controlled. Fourth, we test for increases in the incidence of male parr maturity within populations that cannot be accounted for by changes in growth rate alone.

Statistical Preliminaries

Before assessing the variation in male parr maturity, we determined the accuracy with which estimates of such maturation were made. We tested the hypothesis that mature male parr were randomly distributed within a river. We examined data on the numbers of 1+ males maturing in the Little Codroy River, Newfoundland, collected by A. R. Murray from 1957 to 1963 (Murray 1968a, 1968b). Each sampling site was placed in one of five categories based upon the modal gravel size at the site (group A $<$ 2.5 cm, 2.5 cm $\leq$ group B $<$ 7.6 cm, 7.6 cm $\leq$ group C $<$ 15.2 cm, 15.2 cm $\leq$ group D $<$ 30.5 cm, 30.5 cm $\leq$ group E). A χ^2 test showed that maturation status was not independent of gravel type ($\chi^2 = 18.3$, df = 8, $P = 0.02$). Mature male parr were more common in sites with gravel size suitable for spawning (group B). Similar results were obtained if samples were taken only in August. Thus, the proportion of males that mature at a particular sample site was not an appropriate estimate of male parr maturity for the entire population.

A better estimate can be obtained by considering the male parr that do not mature. Because Atlantic salmon have a 1:1 sex ratio at hatching (Vladimirskaya 1958; Mitans 1973) and mortality before maturation is independent of sex (Myers 1984), the proportion of age 1+ male parr that mature is 1 − (number of immature age 1+ male parr/number of age 1+ female parr). A χ^2 test on the Little Codroy data showed immature males and females to be distributed independently of stream bed type ($\chi^2 = 1.04$, df = 4, $P = 0.90$). We used this new criterion for estimating the proportion of males that mature.

However, within-river heterogeneity still existed (χ^2 test for independence of Little Codroy data, sites with expected cell size less than five eliminated, $\chi^2 = 68.6$, df = 26, $P = 0.0001$). Thus, it is still necessary to account for within-river heterogeneity in any analysis.

The usual assumption in the analysis of binary data, such as maturation of male parr, is that the number of animals in a class, e.g. those that mature, follows a binomial distribution. This is, for example, one of the assumptions of probit models (Finney 1971). This assumption is not valid for the incidence of parr maturation because there is significant within-river variation in this characteristic. To analyse this heterogeneity, we assume that at any one site in a river, the number of sampled males that are mature follows a binomial distribution with parameter p, and that the binomial parameter p varies as a beta distribution with parameters (α, β). That is, the variation in incidence of male parr maturation follows a beta-binomial distribution (Paul and Plackett 1978). If there are n males sampled at m sites, then the variance in mature males is

$$(1) \quad \frac{p\,(1-p)}{mn}\,\frac{(n\epsilon+1)}{(\epsilon+1)}$$

where $\epsilon = 1/(\alpha + \beta)$. Thus, the variance for the beta-binomial distribution is $(n\epsilon + 1)/(\epsilon + 1)$ times the variance of the binomial distribution. If α and β are estimated for a population, then this heterogeneity factor $(n\epsilon + 1)/(\epsilon + 1)$ can be used to adjust the variance computed using the binomial assumption, to the appropriate value needed for meaningful significance tests (Paul and Plackett 1978).

Data were available from the Little Codroy River and the Miramichi River (Schofield and Peppar 1982) to assess within-river heterogeneity. Maximum-likelihood estimates of α and β were obtained using the Nelder−Meed simplex algorithm as described by Griffiths (1973). A heterogeneity factor was computed using the mean sample size per site, $\bar{n}$ (Table 1). The binomial assumption underestimates the variance by as much as one tenth its true value.

Reduction in Growth Caused by Maturation

We estimated the reduction in growth resulting from maturation as parr, taking care to include the observation that males destined to mature as parr have a higher mean growth rate than other males during early gonadal maturation. The fundamental assumption in our estimate was that there would be no difference in growth between male and female parr in the absence of parr maturation. This was tested by examining growth, before maturation occurs, as recorded in the first year scale growth. A two-way analysis of variance, considering yearly variations as well as possible differences between sexes, on 2600 1+ parr yielded no significant variation in growth between males and females ($P > 0.05$).

We wish to estimate λ, the proportional reduction in length resulting from maturation. Thus, on average, a male that ma-

TABLE 2. Fork lengths and reduction in length associated with parr maturation in the Little Codroy River (calculated from Eq. 1).

	Year						
	1957	1958	1959	1960	1961	1962	1963
Mean fork length (mm) (sample size)							
Immature males (m_i)	87.5 (18)	82.9 (25)	85.2 (29)	78.3 (82)	82.5 (89)	82.8 (35)	83.4 (68)
Mature males (m_p)	85.3 (70)	87.8 (93)	86.7 (76)	84.9 (289)	85.7 (120)	88.6 (123)	86.7 (136)
Females (f)	87.1 (70)	88.2 (84)	89.3 (67)	86.6 (338)	87.2 (171)	92.5 (155)	85.4 (199)
Proportion 1+ males maturing (q)	0.795	0.788	0.724	0.776	0.658	0.812	0.677
Proportional reduction in length (λ)	0.019	0.020	0.045	0.046	0.045	0.065	−0.003
Reduction in second year growth (mm)	1.65	1.76	4.02	3.98	3.92	6.01	—

TABLE 3. Relationship between growth and sexual maturation in salmon parr (sample size in parentheses). See text for explanation of how "% mature" was calculated (for "% mature", sample size equals total number of females plus total number of immature males).

River	Fork length (mm) at 1+	% mature	Fork length (mm) at 2+	% mature	Collection method[a]	References[b]
Newfoundland						
Bay de l'Eau	73.1 (52)	72.4 (35)		80.0 (6)	E	1,2
Come By Chance	72.2 (70)	78.6 (34)			E	1,2
Lomond	72.7 (79)	48.6 (56)		100.0 (2)	E	1,2
North Harbour	84.3 (44)	11.8 (32)		80.0 (6)	E	1,2
Rocky	85.4 (45)	16.0 (41)	104.4 (71)	25.6 (68)	E	1,2
Salmon	73.6 (37)	24.0 (31)	100.8 (64)	89.0 (20)	E	1,2
Rushoon	97.2 (18)	100.0 (18)	108.0 (54)	100.0 (33)	E	1,2
Tote	62.5 (6)	80.0 (6)	82.8 (49)	37.5 (39)	E	1,2
Highlands	82.7 (82)	55.0 (58)	109.8 (64)	52.4 (31)	E	3
Little Codroy	85.9 (2574)	71.5 (1654)	115.6 (877)	84.0 (526)	E	3
Northwest	90.5 (45)	95.2 (22)			E	3
Southwest	78.3 (43)	84.0 (29)			E	3
Wings	76.3 (55)	79.3 (35)			E	3
Western Arm	75.4	3.9 (214)	109.0	41.1 (170)	E	3
Quebec						
Bouleau	83.6 (48)	13.0 (86)	112.9 (80)	35.9 (84)	S	4
Pigou	96.2 (53)	37.5 (39)	133.8 (32)	63.1 (26)	S	4
Matamek	85.9 (158)	62.6 (239)	125.6 (292)	64.7 (209)	F,S,A	5,6,7
Corneille	98.9 (39)	38.3 (76)	148.5 (16)	80.0 (36)	S,A	6
Manitou	76.3 (3)	36.0 (3)	114.9 (41)	82.3 (20)	S,A	6
Mistassini	76.1 (47)	9.7 (59)	108.9 (29)	100.0 (26)	S,A	6
Moisie	63.1 (36)	0.0 (388)	89.9 (25)	0.7 (580)	S,A	6
Puyjalon	71.3 (46)	0.0 (45)	117.1 (17)	100.0 (10)	S,A	6
Ste. Marguerite	66.3 (8)	16.7 (11)	93.5 (32)	35.0 (33)	S,A	6
St. Jean	54.2 (23)	0.0 (23)	74.3 (29)	11.1 (34)	S,A	6
Watshishou	89.3 (64)	40.8 (58)	120.2 (35)	25.0 (28)	A,G	8
Nova Scotia						
Margaree	85.8 (82)	75.0 (45)	110.8 (32)	90.9 (12)	E	3
New Brunswick						
Miramichi	93.9 (380)	60.5 (276)	114.4 (210)	63.4 (153)	E	9
Restigouche	82.0 (212)	22.0 (178)	111.0 (30)	68.4 (25)	E	10

[a]E = electrofishing; S = seining; G = gill netting; A = research angling; F = fyke netting.

[b]1, Dalley 1979; 2, Dalley et al. 1983; 3, L. Marshall, Department of Fisheries and Oceans, Halifax, N.S.; 4, Randall and Power 1979; 5, Schiefer 1969; 6, Schiefer 1971; 7, R. J. Gibson, unpubl. data; 8, Riley et al. 1984; 9, Schofield and Peppar 1982; 10, R. Randall, Department of Fisheries and Oceans, Moncton, N.B.

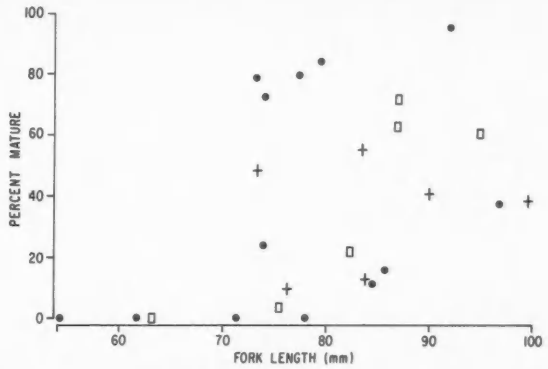

FIG. 1. Proportion of 1+ male parr that mature as a function of mean length of 1+ fish in August for North American rivers listed in Table 3 (populations with sample size between 20 and 50 (●), between 50 and 100 (+), and over 100 (□)).

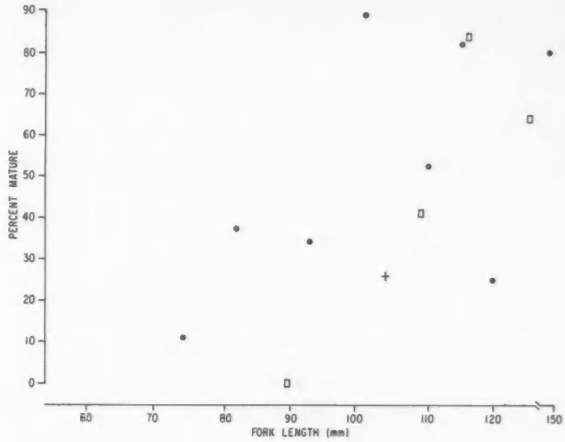

FIG. 2. Proportion of 2+ male parr that mature as a function of mean length of 2+ fish in August for North American rivers listed in Table 3 (populations with sample size between 20 and 50 (●), between 50 and 100 (+), and over 100 (□)).

tures would be 1-λ as long as it would be were it not to mature. If our assumption holds, the mean size of male and female parr at the time some males are maturing is the same, and

$$(2)\quad f = (1 - q)\, m_i + \frac{q}{(1 - \lambda)}\, m_p$$

where f = mean fork length of 1+ female parr, m_i = mean fork length of 1+ immature male parr, m_p = mean fork length of 1+ mature male parr, and q = proportion of mature parr within the male population. Note that $m_p/(1 - \lambda)$ is the mean fork length 1+ mature males would have achieved if they had not matured. The reduction in length was thus estimated to be

$$(3)\quad \lambda = 1 - \frac{q\, m_p}{f - (1 - q)\, m_i}.$$

Data from seven years (1957–63) were available from the Little Codroy River to calculate growth reduction. A comparison of the cumulative distribution of fork lengths of males and females showed that these distributions were significantly different in six of seven years (Kolmogorov–Smirnov test, $P < 0.05$). All years except 1963 showed a reduction in growth of mature males (Table 2). There was an average 4.0% (1.9 – 6.5%) reduction in length (~3.6 mm) associated with male parr maturation. Since this reduction took place only during the second year of life, the reduction in yearly growth during the year the parr matured was approximately 8%.

It is possible that parr maturation alters some other feature of the distribution of fork lengths. To test this hypothesis, each mature 1+ male fork length was multiplied by $1/(1-\lambda)$ and then combined with the distribution of immature male parr. This modified distribution of male fork lengths was compared with the female distribution by quantile–quantile plots (Wilk and Gnanadesikan 1968) and Kolmogorov–Smirnov tests. There was no systematic or significant ($P > 0.05$) deviation of the modified male lengths from the female distribution.

Among-Population Comparisons of Parr Maturation

The purpose of this analysis was to describe the covariation in growth and maturation of male parr among 27 salmon populations in eastern North America (Table 3) and to determine if there were any significant differences among populations in the incidence of male parr maturity once the effect of growth rate had been removed.

To avoid the confounding bias of reduced growth caused by maturation, mean female length was used in the analysis if it was available. If not, then the mean lengths were modified by using the estimated mean proportion of the males maturing, q, observed in the population and the proportional reduction in length caused by maturation, λ. Let the mean length observed in a population be X. We need a coefficient that when multiplied by the mean length observed in the population, X, approximates the mean length of females in the population. If we make the simplifying assumption that immature males grow at approximately the same rate as females, we have

$$(4)\quad X = \tfrac{1}{2}f + \tfrac{1}{2}\{(1 - q)\, f + qf(1-\lambda)\}$$

where, as before, we have assumed a 1:1 sex ratio. A coefficient, γ, is required such that

$$(5)\quad \gamma X = f.$$

Rearranging the above two equations yields the correction factor

$$(6)\quad \gamma = \frac{2}{2 - q\lambda}.$$

There appears to be a size threshold (≈72 mm at the end of the second year of life) below which males are not likely to mature (Fig. 1). Data were log-transformed and analysed using a probit regression (Finney 1971). The slope of the regression was significant ($P < 0.05$), indicating a positive covariation between growth and maturation among rivers. However, the fit of the data to the model was not good ($\chi^2 = 1153.0$, df = 21, $P < 0.0001$). The χ^2 was recalculated after excluding the St. Jean River population (the only population with an expected cell frequency less than five) and was still highly significant ($\chi^2 = 1152.0$, df = 20, $P < 0.0001$). The among-population variation remained high significant ($P < 0.0001$) following application of the maximum heterogeneity factor (5.2).

There was a significant correlation between size and maturation for parr maturing at age 2+ although a size threshold

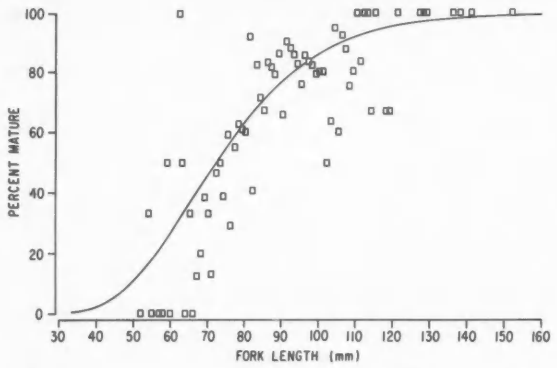

FIG. 3. Maturation versus length relationship of male parr within the Little Codroy population (line represents probit regression of log-transformed data).

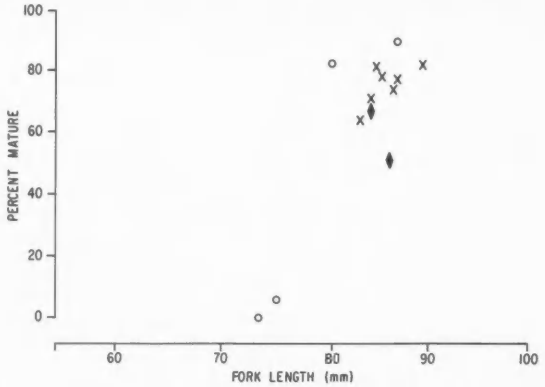

FIG. 4. Proportion of 1+ male parr that mature versus fork length of male parr in the population (Little Codroy River (×), Matamek River below third falls (○), and below fourth falls (◆)). Years in which sample size was less than 10 were not plotted.

was not apparent (Fig. 2). These data should be interpreted with caution, however, because many parr smoltify at age 2.

Within-Population Variation

Size before maturation was estimated for 1275 male parr of the Little Codroy River population (1957–63 years combined). For χ^2 goodness of fit tests, fork length (millimetres) classes were combined such that expected cell frequencies of males exceeded five.

The pattern of length-specific maturation for 1+ parr in the Little Codroy was similar to that observed for the among-population data. The probit analysis indicated a size threshold of ≈70 mm, below which males were not likely to mature (Fig. 3). There was a much better fit of the within-population data to a probit regression on log-transformed length (χ^2 = 122.1, df = 58, $P < 0.0001$) than there was in the among-river comparison.

Yearly Variation in Parr Maturity and Growth

We examined data from the Matamek (1967–78) and Little Codroy (1957–63) rivers, the only two North American populations with time series of data on parr maturation, to determine the degree to which the incidence of parr maturity has varied over time within populations. In both rivers, maturation first occurs at 1+ and smolt ages are predominately 2, 3, and 4 (Murray 1968a, 1968b; Gibson 1978; Myers 1984). Parr used in the Matamek analyses were collected in the areas below the third and fourth falls of this river. Before the successful introduction of non-Matamek salmon fry into the river in 1978 and 1979, only one 1+ mature male parr was collected below the second falls. Furthermore, spawning does not occur below these falls (R. J. Gibson, pers. obs.), and their 7-m height (Power et al. 1973) precludes upstream migration of parr to the spawning grounds. Parr collected below the second falls, then, were excluded from the analyses. Post-1978 data from the Matamek River were excluded because of the successful introductions of non-Matamek salmon fry into the river in 1978 and 1979.

The among-year pattern of variation in parr maturation (Fig. 4) is similar to the within-year pattern for the Little Codroy River (Fig. 3) and the among-population pattern (Fig. 1). Again there appears to be a threshold level of size required for maturation as a parr.

For the Little Codroy River population we could also calculate the proportion of 2+ males that mature as parr for four cohorts because Myers (1984) was able to estimate the mortality associated with parr maturation and the proportion of 1+ and 2+ parr that smolted and matured. Thus, we could determine if there was evidence that yearly changes in growth rate affected the proportion of *all* males that mature as parr within a cohort. We found no evidence that increased growth during the first year of life increased the total proportion of male parr that mature. In fact, the data suggest that increased growth during the first year of life is associated with a decreased proportion of males maturing at age 2 (Fig. 5).

Evolutionary Changes in Parr Maturation

It has been suggested that the proportion of mature male parr increases within populations that experience high mortality at sea (Gibson 1978; Montgomery 1983). One explanation for this increase is that intense fishing pressure should favour those genotypes that mature in freshwater, thereby avoiding mortality at sea (Myers 1983; Caswell et al. 1984). We examined the residuals of the probit regression of percent parr maturity on growth from the Matamek (1967–78) and Little Codroy (1957–63) rivers to determine if that percentage has increased independent of changes in growth rate. A plot of the residual variation in parr maturation, using the probit regression generated from the Little Codroy River population, shows no obvious pattern with time for the Matamek population (Fig. 6). Similarly, there was no apparent trend with time in the residuals in the Little Codroy River population. The robustness of our conclusions were tested by calculating the residuals from the among-river (Fig. 1) and within-population (Fig. 4) probit regressions of maturity on length. Again, no relationship with time was evident.

Discussion

There is a common pattern in the covariation of maturation and growth in salmon parr within and among populations and among years; few male parr mature below 70–72 mm in

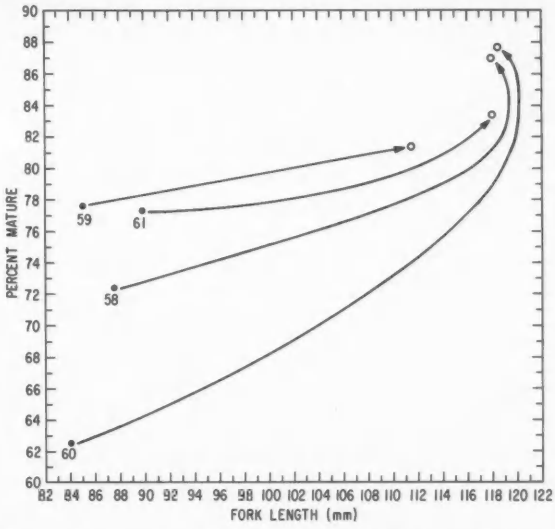

FIG. 5. Incidence of maturity for 1+ male parr (●) and the incidence for 1+ and 2+ parr (○) versus the mean length of 1+ and 2+ parr for the Little Codroy population. Data are plotted by year of hatching.

length. Although the idea that there is a "critical length" for maturation is clearly simplistic, it is an adequate first approximation in describing parr maturation. Perhaps this critical length is required before sufficient energy stores are available for maturation and subsequent winter survival. This hypothesis could be tested by examining the distribution of sizes of mature males before reproduction, e.g. in August, and after winter survival in the spring. If there is size-dependent overwinter survival, then there should be a shift in the size distribution of summer-to-spring samples. An alternative hypothesis is that parr size is crucial in the establishment of the dominance hierarchy among male parr downstream of a spawning sea-run pair (Myers and Hutchings 1986). This hypothesis could be tested by examining the proportion of eggs fertilized by mature male parr of different sizes using electrophoretic markers.

Although growth has a great effect on the proportion of males that mature at 1+, it is clearly not the only factor involved. The highly significant χ^2 values from the probit regressions, which resulted after accounting for length effects and data heterogeneity, suggest that a large amount of the variation in maturation cannot be explained by length alone. The significant heterogeneity within populations is consistent with evidence for additive genetic variation in parr maturation (Naevdal et al. 1976). Similarly, the great among-population variation in parr maturation suggests either that the evolutionary pressures on parr maturation vary among populations or that alternative evolutionarily stable strategies exist within populations (Myers 1986). The evolutionary mechanism leading to this among-river variation warrants further study.

Although among-year variation in growth during the first year of life affects the proportion of 1+ males that mature, we found no evidence that increases in growth rates increase the total proportion of male parr that mature within a year-class, since a male parr not maturing at 1+ may mature later. Such factors need to be considered in constructing stock–recruitment models.

Changes in the proportion of male parr maturing in the

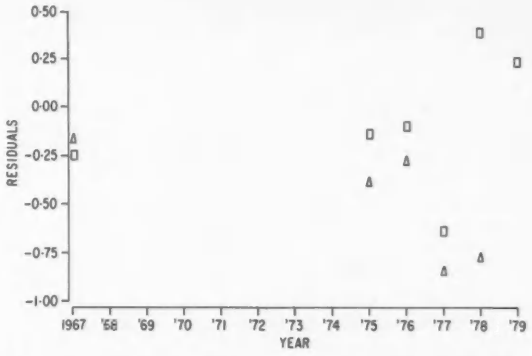

FIG. 6. Residuals from probit regression (from Little Codroy population, see Fig. 3) of proportion mature versus length in the first year, by year, in the Matamek River (□, third falls; △, fourth falls).

Matamek River population can be accounted for by changes in growth alone. There is no evidence that the proportion of mature parr in the Matamek that has been increasing in recent years is a genetic change caused by increased commercial fishing pressures as proposed by Montgomery (1983) and Caswell et al. (1984), who did not consider the relationship between growth and maturation. Given a generation time of 4 – 5 yr for Atlantic salmon, significant short-term (5 – 15 yr) increases in the proportion of mature parr in a population would reflect extremely high selection intensities and heritabilities for parr maturation.

It is difficult, r impossible, to achieve random sampling in rivers because of extreme among-site variation. We have mitigated this problem by estimating the degree of heterogeneity in the proportion of males maturing in two intensively sampled rivers, and using this "heterogeneity factor" to interpret the accuracy of our data. It was found that the assumption of simple random sampling was not appropriate for our data but that quantitative comparisons could be made once the heterogeneity was accounted for. Spurious results could arise from a failure to utilize such within-population information.

Acknowledgments

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References

ALM, G. 1959. Connection between maturity, size and age in fishes. Inst. Freshwater Res. Drottningholm Rep. 40: 5–145.

CASWELL, H., R. J. NAIMAN, AND R. MORIN. 1984. Evaluating the consequences of reproduction in complex salmonid life cycles. Aquaculture 43: 123–134.

DALLEY, E. L. 1979. Studies on the biology of sexually mature male salmon parr, *Salmo salar* (Linnaeus) 1758, in insular Newfoundland. M.Sc. thesis, Memorial University of Newfoundland, St. John's, Nfld. 106 p.

DALLEY, E. L., C. W. ANDREWS, AND J. M. GREEN. 1983. Precocious male Atlantic salmon parr (*Salmo salar*) in insular Newfoundland. Can. J. Fish. Aquat. Sci. 40: 647–652.

FINNEY, D. J. 1971. Probit analysis. 3rd ed. Cambridge University Press, London. 333 p.

GIBSON, R. J. 1978. Recent changes in the population of juvenile Atlantic salmon in the Matamek River, Québec, Canada. J. Cons. Int. Explor. Mer 38: 201–207.

GRIFFITHS, D. A. 1973. Maximum likelihood estimation for the beta-binomial distribution and an application to the household distribution of the total number of cases of a disease. Biometrics 29: 637–648.

JONES, J. W. 1959. The salmon. Collins, London. 192 p.

LEYZEROVICH, KH. A. 1973. Dwarf males in hatchery propagation of the Atlantic salmon (*Salmo salar* L.). J. Ichthyol. 13: 382–392.

MITANS, A. R. 1973. Dwarf males and the sex structure of a Baltic salmon (*Salmo salar* L.) population. J. Ichthyol. 13: 192–197.

MONTGOMERY, W. L. 1983. Parr excellence. Nat. Hist. 92: 58–67.

MURPHY, T. M. 1980. Studies on precocious maturity in artificially reared 1+ Atlantic salmon parr *Salmo salar* L. Ph.D. thesis, University of Stirling, Scotland. 2 vols.

MURRAY, A. R. 1968a. Smolt survival and adult utilization of Little Codroy River, Newfoundland, Atlantic salmon. J. Fish. Res. Board Can. 25: 2165–2218.

1968b. Numbers of Atlantic salmon and brook trout captured at the Little Codroy River, Newfoundland, counting fence and auxiliary traps, 1954–63. Fish. Res. Board Can. Tech. Rep. 84: 135 p.

MYERS, R. A. 1983. Evolutionary change in the proportion of precocious parr and its effect on yield in Atlantic salmon. Int. Counc. Explor. Sea C.M.1983/M:14: 16 p.

1984. Demographic consequences of precocious maturation of Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. 41: 1349–1353.

1986. Game theory and the evolution of Atlantic salmon (*Salmo salar*) age at maturation, p. 53–61. *In* D. J. Meerburg [ed.] Salmonid age at maturity. Can. Spec. Publ. Fish. Aquat. Sci. 89: 118 p.

MYERS, R. A., AND J. A. HUTCHINGS. 1986. Mating of anadromous Atlantic salmon, *Salmo salar* L., with mature male parr. J. Fish Biol. (In press)

NAEVDAL, G., M. HOLM, D. MOLLER, AND O. D. OSTHUS. 1976. Variation in growth rate and age at sexual maturity in Atlantic salmon. Int. Counc. Explor. Sea C.M.1976/E:40: 10 p.

PAUL, S. R., AND R. L. PLACKETT. 1978. Inference sensitivity for Poisson mixtures. Biometrika 65: 591–602.

POWER, G., F. G. POPE, AND B. W. COAD. 1973. Postglacial colonization of the Matamek River, Quebec, by fishes. J. Fish. Res. Board Can. 30: 1586–1589.

RANDALL, R. G., AND G. POWER. 1979. Atlantic salmon (*Salmo salar*) of the Pigou and Bouleau Rivers, Quebec. Environ. Biol. Fishes 4: 179–184.

RILEY, S. C., A. T. BIELAK, AND G. POWER. 1984. The Atlantic salmon stock of the Grand Watshishou River (Québec) — a historical perspective. Nat. Can. 111: 219–228.

SAUNDERS, R. L., E. B. HENDERSON, AND B. D. GLEBE. 1982. Precocious sexual maturation and smoltification in male Atlantic salmon (*Salmo salar*). Aquaculture 28: 211–229.

SAUNDERS, R. L., AND C. P. SCHOM. 1985. Importance of the variation in life history parameters of Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. 42: 615–618.

SCHIEFER, K. 1969. Ecology of Atlantic salmon, *Salmo salar* L., in the Matamec River system. M.Sc. thesis, University of Waterloo, Waterloo, Ont. 63 p.

1971. Ecology of Atlantic salmon, with specific reference to occurrence and abundance of grilse in North Shore Gulf of St. Lawrence rivers. Ph.D. thesis, University of Waterloo, Waterloo, Ont. xvi + 129 p.

SCHOFIELD, E. J., AND J. L. PEPPAR. 1982. Some biological statistics on Atlantic salmon parr from the Miramichi River system, New Brunswick. Can. Data Rep. Fish. Aquat. Sci. 322: vii + 15 p.

THORPE, J. E., R. I. G. MORGAN, C. TALBOT, AND M. S. MILES. 1983. Inheritance of developmental rates in Atlantic salmon, *Salmo salar* L. Aquaculture 33: 119–128.

VLADIMIRSKAYA, M. I. 1958. Young salmon in the upper part of the River Petchora. Int. Counc. Explor. Sea 148: 53–57.

WILK, M. B., AND R. GNANADESIKAN. 1968. Probability plotting methods for the analysis of data. Biometrika 55: 1–17.

Winter Hydrography and Plankton Distribution on the Southern British Columbia Continental Shelf

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Thomas, A. C., and W. J. Emery. 1986. Winter hydrography and plankton distribution on the southern British Columbia continental shelf. Can. J. Fish. Aquat. Sci. 43: 1249–1258.

The early winter (November–December 1983) concentrations and spatial distributions of chlorophyll and zooplankton on the southern British Columbia continental shelf are shown to be closely related to patterns of hydrographic parameters. Concentrations of both are an order of magnitude less than published summer values for the same area. On the basis of hydrographic and planktonic characteristics, the continental shelf region can be divided into an area dominated by the Vancouver Island Coastal Current and one dominated by the northward flowing Davidson Current which can be isolated in the data and traced along the outer shelf edge. Highest chlorophyll and zooplankton concentrations (1.0 mg·m^{-3} and 2900 counts·m^{-3}) were found in Coastal Current water and the frontal zone between this and the Davidson Current water. The warmer Davidson Current water was associated with extremely low chlorophyll and zooplankton concentrations (<0.2 mg·m^{-3} and <1700 counts·m^{-3}). The spatial distributions of both chlorophyll and zooplankton reflected variations in the cross-shelf position of the Davidson Current which appeared to be topographically controlled. Contours of sea surface temperature, inferred from hydrographic data, were similar to contours of chlorophyll and zooplankton concentration. Both in situ temperature and plankton distributions were spatially consistent with thermal patterns in concurrent high-resolution satellite infrared imagery. Areas of increased surface thermal gradient were consistent with in situ measured biological fronts.

Les auteurs montrent que les concentrations et les distributions spatiales de début d'hiver (novembre et décembre 1983) de la chlorophylle et du zooplancton de la partie sud du plateau continental de la Colombie-Britannique présentaient des allures très similaires à celles de certains paramètres hydrographiques. Les deux concentrations étaient d'un ordre de grandeur inférieures aux valeurs d'été mentionnées dans la littérature pour cette région. Les caractéristiques hydrographiques et planctoniques permettent de diviser cette région du plateau continental en deux zones : l'une dominée par le courant côtier de l'île de Vancouver et l'auteur dominée par le courant Davidson, de direction nord, qui peut être délimité à partir des données et localisé le long de la bordure externe du plateau. Les concentrations de chlorophylle et de zooplancton les plus élevées (1,0 mg·m^{-3} et 2 900 unités·m^{-3}) ont été notées dans le courant côtier et le front le séparant du courant Davidson. Les eaux plus chaudes du courant Davidson présentaient des concentrations de chlorophylle et de zooplancton extrêmement faibles (< 0,2 mg·m^{-3} et <1 700 unités·m^{-3}). Les distributions spatiales de ces deux paramètres reflétaient les variations probablement dues à la topographie du trajet du courant Davidson qui coupe transversalement le plateau. Les courbes de valeurs égales de la température à la surface de l'eau, obtenues à partir de données hydrographiques, étaient similaires à celles des concentrations de la chlorophylle et du zooplancton. Les distributions des températures et des concentrations planctoniques déterminées sur place correspondaient aux distributions thermiques déterminées au même moment par imagerie infrarouge haute résolution obtenue par satellite. Les zones de gradients thermiques de surface accrus correspondaient aux fronts biologiques délimités sur place.

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In northern and temperate latitudes, low incident light and low temperatures during the winter increase the time scales of such biological processes as grazing, nutrient uptake, and reproduction, making planktonic distributions during this period primarily a function of the physical regime. The winter plankton distribution is therefore determined primarily by the physical properties in the study area.

Winter concentrations and spatial distributions of phytoplankton and zooplankton on the southwestern British Columbia continental shelf have not been previously described. While this area (see Fig. 1) has been the subject of earlier studies both on the spatial distribution of plankton (Mackas et al. 1980) and the processes governing that distribution (Denman et al. 1981), they all dealt specifically with summer conditions. Freeland and Denman (1982) and Denman et al. (1981) showed that summer upwelling of deep water has an important influence on phytoplankton productivity and distribution, and possibly even fish distribution, but does not occur regularly during the winter. Stefansson and Richards (1963) and Mackas et al. (1980) have shown that interactions between the estuarine circulation at the mouth of Juan de Fuca Strait and tidal advection, upwelling, and the complex bottom topography result in a productive, but spatially variable, summer nutrient and plankton regime. Mackas and Sefton (1982) suggested that this summer commu-

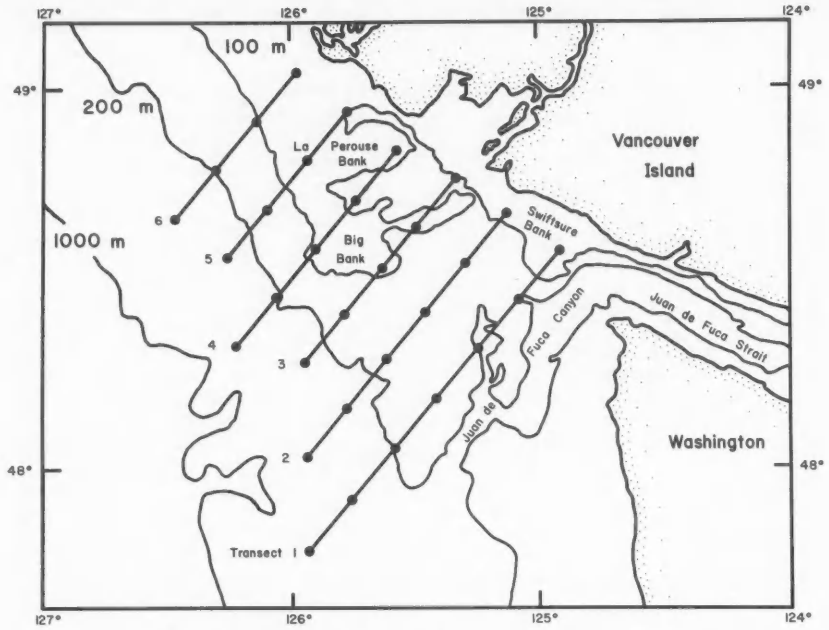

FIG. 1. Study area showing depth contours, major topographic features, sampling transects, and the positions of stations along the transects used for vertical profiles.

nity structure is primarily a function of extraneous succession and advection.

The outer continental shelf and offshore waters of Washington State and British Columbia are part of the California Current System, with winter surface flow in a northwest direction (Hickey 1979). Descriptions of the winter temperature regime in the study area were given by Douglas and Wickett (1978) and Dodimead and Ballantyne (1980). Freeland et al. (1984) showed the existence of a strong seasonal cycle in the current regime, with winter conditions dominated by northwest currents on the outer shelf and a runoff-driven coastal current in the same direction along the inner shelf. Satellite infrared images show seasonal variability in the length scales of meanders and eddies in the California Current System off the west coast of Vancouver Island, with topography initiating features of a specific wavelength (Ikeda et al. 1984).

Our primary objective was to relate winter physical conditions, represented by sea surface temperature and subsurface hydrography, to coincident winter distributions of chlorophyll and zooplankton. A second objective was to suggest possible connections between these distributions and local bottom topography. Previously published summer surveys (referenced earlier) allow a comparison between our winter data and summer conditions.

The horizontal description of the surface temperature regime is supplemented by coincident infrared satellite imagery. The resolution of this imagery and the spatial scale of the cross-shelf in situ sampling impose a minimum length scale of approximately 2 km on the size of features which can be resolved. Along-shelf in situ spatial scales are 10 times this distance. The study is therefore a coarse-scale comparison of winter biological and physical parameters and by necessity cannot be a detailed study of spatial correlations or an analysis of higher frequency temporal or spatial fluctuations.

Methods

Data collection for the study involved the simultaneous recording and processing of infrared satellite imagery and ship-measured in situ data. A series of six ship transects (see Fig. 1) perpendicular to the coast were sampled during the period from November 28 to December 5, 1983. The transects were 18.5 km apart, each starting in shallow nearshore water and extending offshore to approximately the 500-m depth contour. These transects were each sampled twice, first to map the surface horizontal distribution of hydrographic and biological properties and second to profile the vertical distribution of hydrographic properties.

Horizontal samples were taken from a depth of 1.5 m using a continuous-flow, high-resolution automated sampling system which counts particles (an estimation of zooplankton concentration) and records temperature, salinity, and fluorescence. A detailed description of the apparatus and its use was given by Mackas et al. (1980) and will not be repeated here. Discrete samples were taken off the apparatus approximately every 15 km along the transects and used for instrument calibration and later nutrient analysis. Fluorescence was converted to chlorophyll concentration and used as a measure of phytoplankton biomass. Nutrient samples were frozen on board and later analysed for nitrates (plus nitrites) and phosphates using an Auto Analyser according to the methods described by Armstrong et al. (1967) and Hager et al. (1968). Vertical profiles of temperature and salinity were measured with a Guildline CTD at stations 18.5 km apart along each transect. The locations of these stations are shown in Fig. 1.

Differences between surface temperatures recorded by the automated sampler and the CTD (RMS difference 0.76°C) can be attributed to a number of causes. (1) The automated sampler has a positive offset (≈0.5°C, Mackas et al. 1980) due to

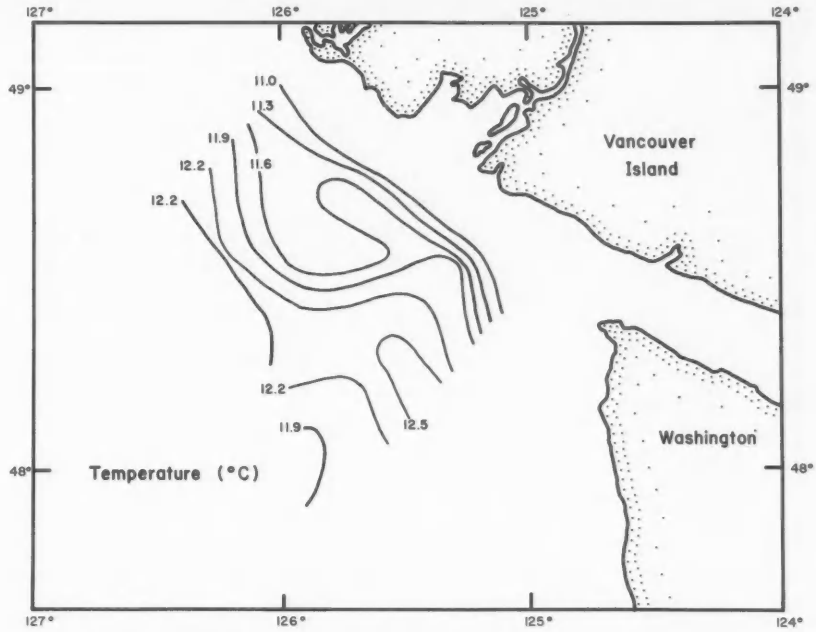

FIG. 2. Sea surface temperature contoured from automated sampling system data taken along the transects.

warming in the plumbing system. (2) Near-surface CTD temperature measurements are less representative due to mixing by the ship and rough seas. (3) There are likely to be small navigational errors in the positions of both the horizontal transects and the vertical stations. (4) Automated sampler surface temperatures were averaged over 1 km, whereas CTD measurements were taken at a specific location. (5) Time lags between horizontal sampling and vertical sampling varied between 1 and 12 h, depending on the length of the transect. Horizontal advective processes and/or vertical mixing during this period might have altered the near-surface thermal regime. The series of satellite images recorded for this survey, however, show that temporal changes in the thermal field on the continental shelf were minimal over the study period. Comparisons between vertical profiles and horizontal contours should therefore be between structure and pattern rather than absolute temperature values.

At a cruising speed of 18.5 $km \cdot h^{-1}$, the spatial resolution of the automated sampling system is approximately 300 m. The data record was first manually despiked and then averaged into 1-km blocks to give a single data point per kilometre along the transects for each of the four variables. As the maximum resolution of the infrared imagery is approximately 1 km, it was felt that such a smoothing procedure would result in little loss of information at the spatial scales with which the study deals.

Infrared imagery from NOAA 7 and 8 were recorded, navigated, and processed to the form presented in this paper at the University of British Columbia Satellite Oceanography Laboratory. Each image was enhanced such that higher brightness values represent colder temperatures and maximum thermal contrast could be seen in the ocean. The Advanced Very High Resolution Radiometer (AVHRR) on NOAA satellites has a thermal resolution of 0.2°C and a nadir spatial resolution of 1.1 km. Land was uniformly masked black and clouds identified and labelled. A series of 10 relatively cloud-free images of the west coast of Vancouver Island were recorded during the study period.

Results

Surface temperatures recorded in situ ranged from 10.6°C near the coast to 12.6°C over the outer shelf. Surface salinity near shore was 29.2 and increased to 32.4 at the seaward edge of the study area. Contour maps of sea surface temperature and salinity are shown in Fig. 2 and 3. Nearshore low-temperature, low-salinity water is separated from warmer, more saline water along the outer continental shelf by a frontal zone across the entire study area. The width of this coastal water is greatest near the mouth of Juan de Fuca Strait; however, a tongue can be seen extending offshore in the vicinity of La Perouse and Big Bank (see Fig. 1). Within the warmer water seaward of the front (average temperatures >11.8°C) is a zone of maximum temperature (>12.2°C). The greatest penetration of warm water onto the shelf is in the vicinity of transect 2. North of transect 3, the warmest water again occupied only the outer shelf area, seaward of the shallow banks.

The positions of surface thermal features revealed by the infrared imagery substantiate those contoured from the in situ transects of sea surface temperature. Figure 4 shows the image recorded on November 30, 1983. The warmest water identified in Fig. 2 can be seen as a dark band over the outer shelf extending in a northwest direction through the study area. Cooler water is seen farther offshore and the coldest water is present along the coast and in Juan de Fuca Strait. The position of the sampled transects has been superimposed on the image to emphasize the study area. Both the intrusion of warm water

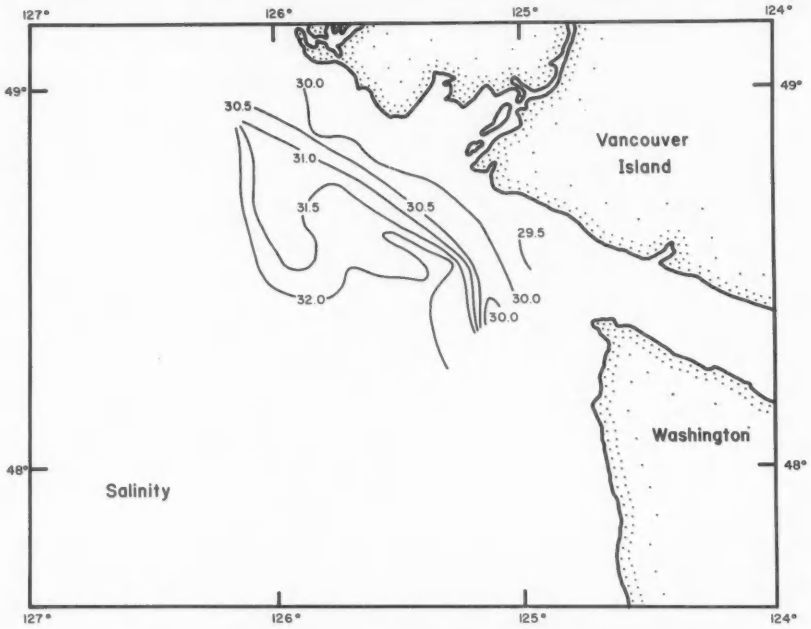

FIG. 3. Surface salinity contoured from automated sampling system data.

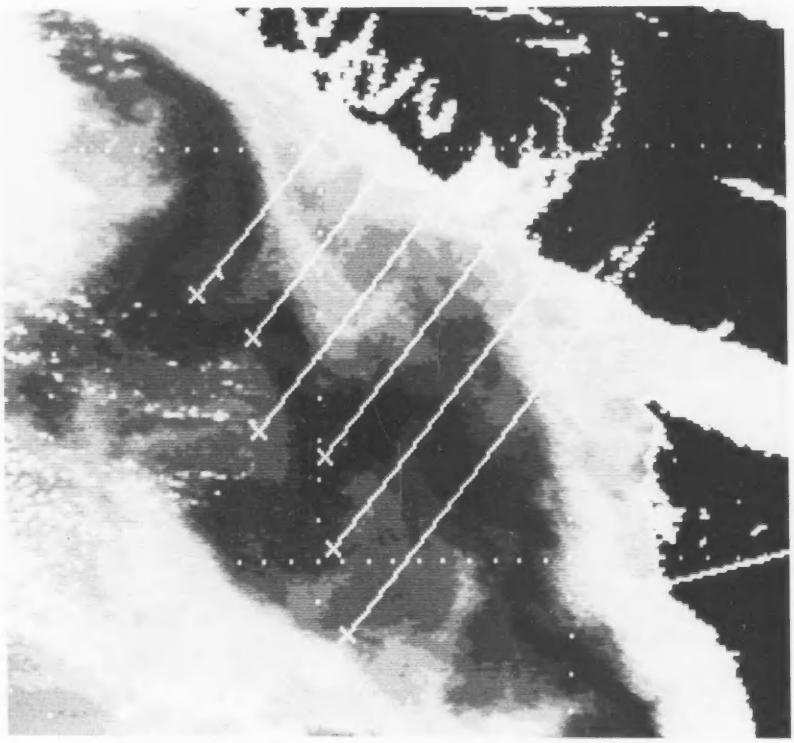

FIG. 4. Satellite infrared image recorded at 15:24 PST on November 30, 1983. Land has been masked black. Some scattered clouds appear on the far left side. Warmest areas are shown as the darkest tones and colder areas as lighter tones. Transect positions have been superimposed.

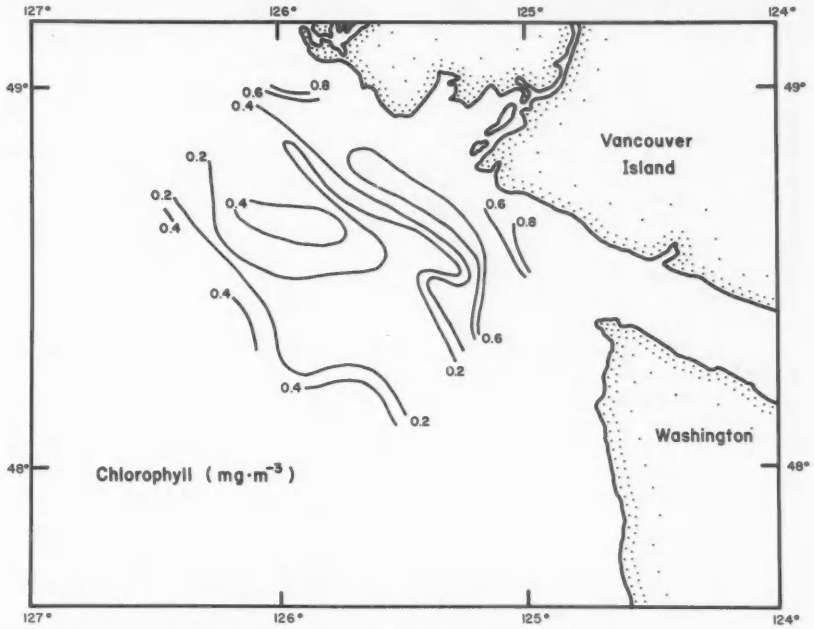

FIG. 5. Surface chlorophyll concentration contoured from automated sampling system data.

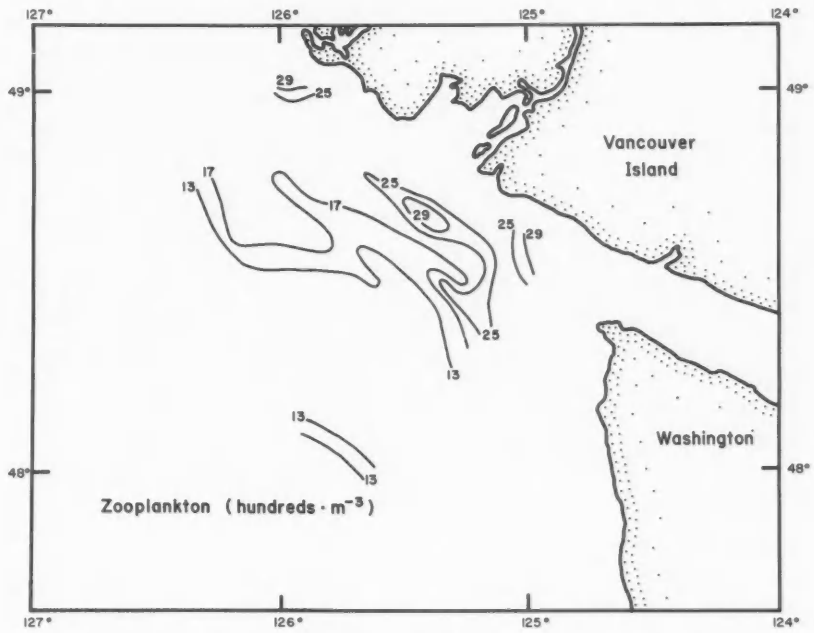

FIG. 6. Surface zooplankton concentration contoured from automated sampling system data.

onto the shelf near transect 2 and the tongue of cold coastal water extending offshore over La Perouse Bank and Big Bank can be identified in the image. The strong thermal gradient indicative of the frontal zone is an obvious feature running parallel to the coast.

The correlation between infrared brightness values and in situ temperature for two representative transects (1 and 2) was 0.91 ($p = 0.99$, df = 198). The extremely high correlation between the two measures of sea surface temperature allows the relative brightness values of the infrared imagery to be used as a visual aid in both extrapolating and interpolating thermal spatial features recorded in situ. Imagery was used only as a

synoptic thermal map for comparative purposes, and all water temperatures reported in this paper were measured in situ.

The general distribution of phytoplankton biomass (Fig. 5) shows a distinct similarity to the surface thermal spatial pattern (Fig. 2 and 4). Maximum chlorophyll values of 1.2 $mg \cdot m^{-3}$ were recorded over the shallow banks in the nearshore low-temperature, low-salinity water. A second area of higher chlorophyll (concentrations above 0.6 $mg \cdot m^{-3}$) coincided with the temperature and salinity front separating the nearshore water from the outer shelf and offshore water. A zone of chlorophyll concentrations below 0.2 $mg \cdot m^{-3}$ was found in the region of highest temperature along the outer shelf. Seaward of this zone, chlorophyll values increased coincident with the surface temperature decrease marking the transition between water of the thermal maximum (>12.2°C) and that of more general offshore conditions (average temperatures 11.8°C).

Nutrients probably play a negligible role in determining both the productivity and the distribution of phytoplankton on the shelf during winter. Nitrate (plus nitrite) concentrations were never less than 1.4 $\mu mol \cdot L^{-1}$ in the study area, with levels above 4.0 $\mu mol \cdot L^{-1}$ in the coastal water. These levels are far above those which would result in nutrient limitation (see MacIsaac and Dugdale 1969). Phosphate levels were highest in coastal water (above 1.3 $\mu mol \cdot L^{-1}$) and never less than 1.0 $\mu mol \cdot L^{-1}$ in the study area. Phosphate is rarely limiting in marine systems and is not likely to be in this case.

The spatial distribution of zooplankton (shown in Fig. 6) was similar to that of chlorophyll, with maximum numbers (over 2900 counts $\cdot m^{-3}$) in the shallow, nearshore coastal areas. A peak (over 2500 counts $\cdot m^{-3}$) coincided with the steepest temperature and salinity gradients and the peak in chlorophyll concentration. The zooplankton spatial pattern seaward of this frontal zone was less clearly defined, but values were always less than 1700 counts $\cdot m^{-3}$. Higher zooplankton counts were found over La Perouse Bank and Big Bank coinciding with both the tongue of cold coastal water extending over this area and the seaward extension of higher chlorophyll values over the banks.

Vertical sections of temperature (Fig. 7) and salinity (not shown) along each transect show that the position of the warmest surface water identified in Fig. 2 and 4 is related to a warm subsurface core of water. In Fig. 7a (transect 1) the 11.5°C isotherm completely isolates the warmest water as a core centered over the outer continental shelf. Salinity contours of the transects show the warm water to be bounded by the 31.75 and the 32.5 isohalines. At transect 2 (Fig. 7b), warmer water occupies almost the entire shelf area. The warm water at transect 3 (Fig. 7c) can be seen to occupy the trough on the landward side of the southern portion of Big Bank (see Fig. 1) partially isolating a pool of colder surface water over the shallow bank. At transect 4 (Fig. 7d) the warm water surfaces at the second station, completely isolating colder coastal water over the shallow bank. The warm-water core is again visible on the outer edge of the shelf, in agreement with Fig. 4. The satellite image confirms that the surface expression of the warm water, in transect 4, has moved farther offshore than in the previous two transects and that the warm water intruding into the nearshore trough does not penetrate farther north than the topographic limit of this feature, just south of transect 5.

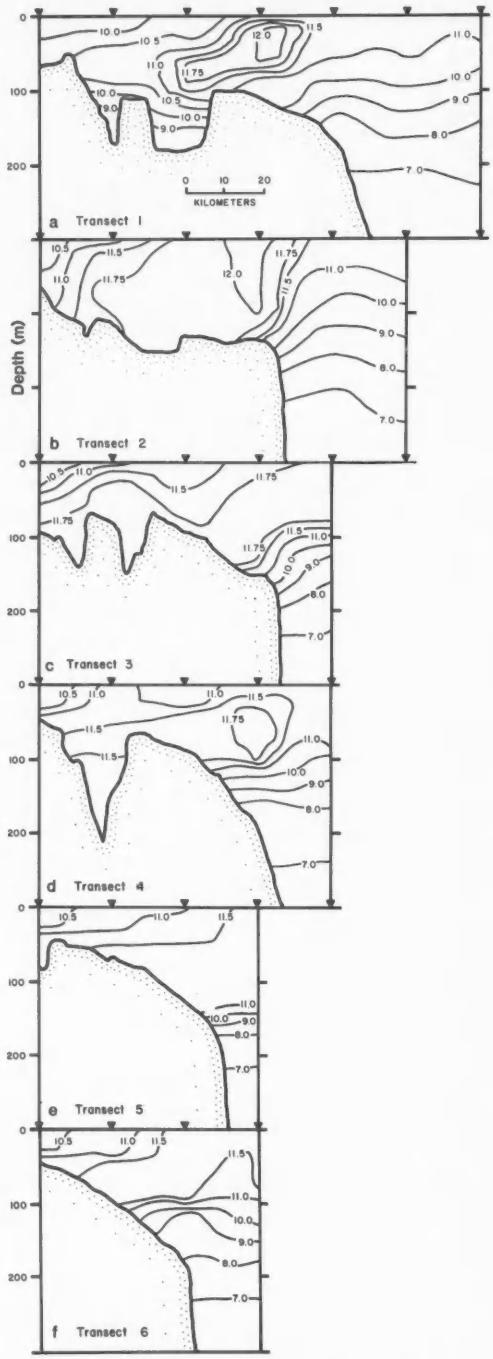

FIG. 7. Vertical temperature sections and bathymetry through each of the transects shown in Fig. 1. Station locations used to contour this data are shown at the top of each section.

Discussion

The warm water over the outer continental shelf in Fig. 2, 4, and 7 was probably a surface expression of the winter northward flow of water in the California Current System (Cannon et al. 1975). Current meter data analyzed by Freeland et al.

(1984) supported Hickey's (1979) description of the northwestward flowing Davidson Current off Cape Mendocino (California) and off the Oregon coast as being continuous up to Vancouver Island in the winter. Ikeda et al. (1984) have previously identified the Davidson Current in winter satellite images of the west coast of Vancouver Island.

Although the hydrographic properties of the water in the warm core are warmer and less saline than those given by Hickey (1979) for Davidson Current water off California, the warm temperature does denote a southern, surface origin, and the low salinity a coastal association. The influence of the Columbia River on winter water properties near Vancouver Island has previously been noted by Lewis (1978). This "upstream" freshwater source might measurably reduce the salinity of the Davidson Current water off Vancouver Island. Hydrographic differences could also be due to the anomalous effects of the 1982–83 "El Niño" event (Emery and Hamilton 1985). Simpson (1983) showed the temperature in the upper 200 m off California in 1983 to be as much as 4°C above the long-term seasonal mean for that area. Freeland et al. (1984) have called the low-temperature, low-salinity coastal water the Vancouver Island Coastal Current and presented arguments for its driving mechanism to be buoyancy input from Juan de Fuca Strait and Vancouver Island coastal rivers.

Winter plankton concentations exhibit a strong quantitative relationship with surface hydrographic properties. Low chlorophyll and zooplankton concentrations are associated with the warmest water (above 12.0°C) in the study area, while the highest concentrations are associated with cooler (less than 11.5°C) and fresher (salinity less than 30.5) water (Fig. 8 and 9). Hydrographically, surface water in the study area can be divided into three regimes. Vancouver Island Coastal Current water is identifiable as water less than 11.5°C with a salinity less than 30.5. Figures 8 and 9 show this water to be associated with high but variable chlorophyll and zooplankton concentrations. The more saline water can be divided into two regimes based on temperature. Davidson Current water is the warmest water on each transect. Clearly associated with this water are the lowest chlorophyll concentrations and lower zooplankton concentrations. The mixing regime between this water and coastal current water becomes more developed in the more northern transects (Fig. 8B, 8C, 9B, and 9C), with lower plankton concentrations associated not only with the warmest water, but also the mixed water of intermediate temperature and salinity. A third hydrographic regime of saline (above 32.0°C) but slightly cooler temperatures (less than 12.0°C) represents general North Pacific water seaward of the Davidson Current. This regime is seen only in Fig. 8A, 8B, 9A, and 9B. Figure 4 confirms that only transects 1, 2, and 4 extend completely across the Davidson Current into this water. The low chlorophyll concentrations found in Davidson Current water are never found in North Pacific water. Zooplankton concentrations associated with this water are always low.

The increase in chlorophyll and zooplankton concentration in the frontal region between Davidson Current water and Coastal Current water is most likely a result of convergence. Two explanations for the high plankton levels in Coastal Current water can be hypothesized. High chlorophyll and zooplankton concentrations found in the Vancouver Island Coastal Current water may have been advected into the area from "upstream," in this case, Juan de Fuca Strait. Chlorophyll concentrations observed by Lewis (1978) in November and December in the upper water column of Juan de Fuca Strait are

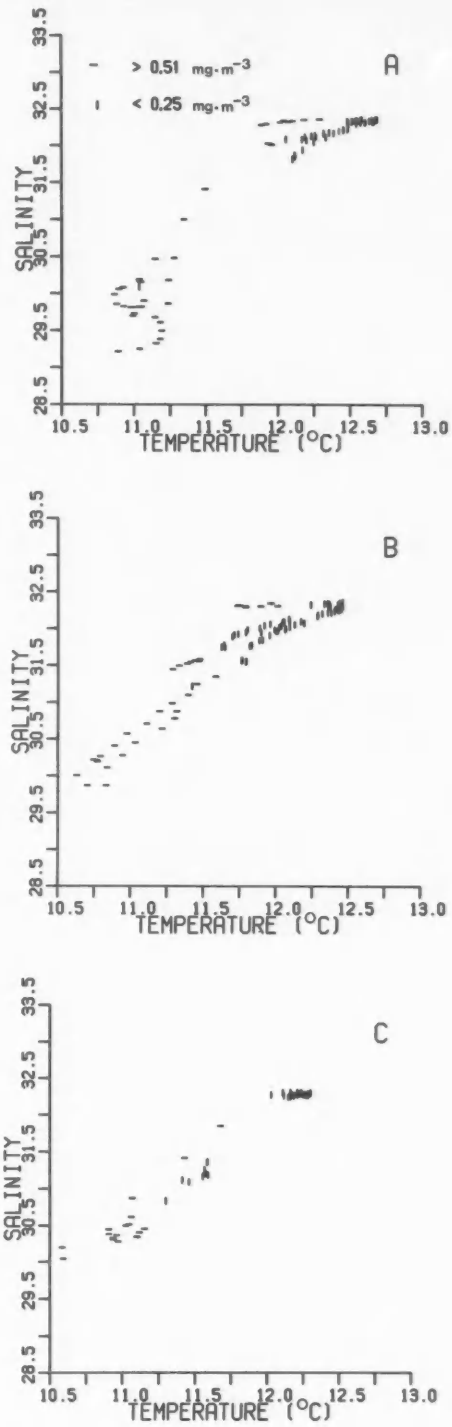

FIG. 8. Relationship between chlorophyll concentration and temperature and salinity. (A) Transects 1 and 2; (B) transects 3 and 4; (C) transects 5 and 6.

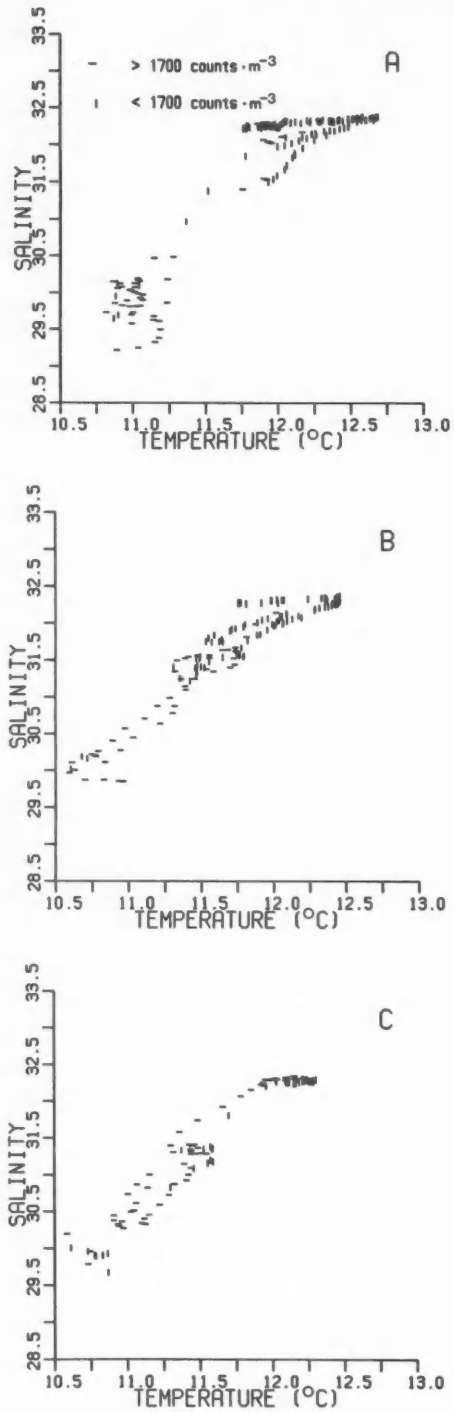

FIG. 9. Relationship between zooplankton concentration and temperature and salinity. (A) Transects 1 and 2; (B) transects 3 and 4; (C) transects 5 and 6.

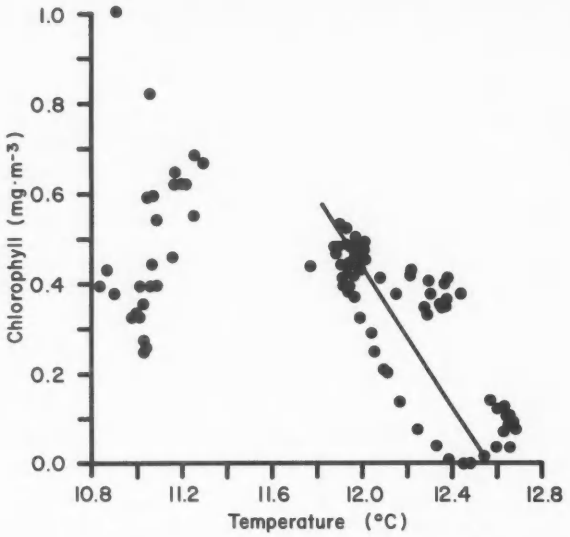

FIG. 10. Relationship between surface temperature and chlorophyll in water on each side of the front, showing a least squares regression line through points seaward of the front (correlation coefficient $r = -0.814$, $p = 0.99$). Only transect 1 data are shown for clarity. Other transects show a similar relationship with varying coefficients.

virtually identical to those found on the shelf in the Coastal Current water during this study. Unfortunately, no previous winter zooplankton data are available for comparison. Higher chlorophyll levels might also be the result of increased productivity in the Coastal Current. Nutrient concentrations on the shelf were not limiting. It is reasonable to assume, then, that low light intensity controls phytoplankton production in the winter. In the winter, when nutrients are not limiting, any increased vertical stability will reduce the mixed depth, increasing light availability and therefore production rates (see Fournier et al. 1979). Areas that are more stratified during the winter due to buoyancy input might thus be zones of increased production. Providing advective processes are slow enough to allow accumulation, even though primary production is still low by summer standards, an increase in phytoplankton biomass will occur over long time periods. An indication of the relative stability of the surface water column can be obtained by calculating the mixed layer depth, defined here as the depth at which the density increased 3.0×10^{-4} g·cm^{-3} above the surface value. This increment was chosen because the most stable pycnocline observed in the area has an increase of similar magnitude. Areas where this depth is less than 50 m are spatially consistent with areas occupied by Coastal Current water and zones of higher chlorophyll concentration. An anomalous point was found in the center of transect 1 where a relatively shallow mixed layer coincided with very low chlorophyll levels. This surface stratification, however, was due not to freshwater buoyancy input, but to the subsurface core of the relatively dense Davidson Current. Strong advection at this point probably prohibited the accumulation of biomass resulting from any enhanced productivity.

A strong relationship between chlorophyll concentration and physical processes is indicated by correlations between temperature and chlorophyll. In low-temperature Coastal Current water, chlorophyll concentrations are most variable, and the

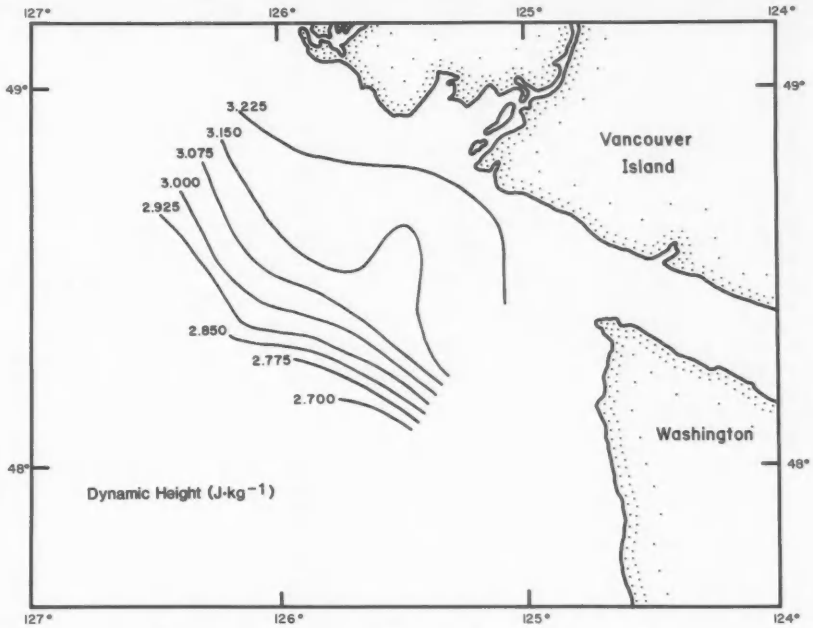

FIG. 11. Contour of dynamic height at 10 m relative to 100 m.

correlation with temperature is low. Seaward of the frontal zone, however, higher temperatures are significantly correlated ($r = -0.814$, $p = 0.99$) with lower chlorophyll values (Fig. 10). No such relationship could be found in the zooplankton data.

The similarity between sea surface isotherms and depth contours (Fig. 1, 2, and 4) suggests an interaction between the position of Davidson Current water on the shelf and bottom topography. While the explanation is speculative, contours of dynamic height (Fig. 11) allow an interpretation of the isotherms presented in Fig. 7. The northwestward flowing Davidson Current penetrates onto the shelf in the southern portion of the study area (Fig. 7A, 7B, and 7C). The shallow areas of La Perouse Bank and Big Bank restrict this penetration except in deeper areas on their landward side. The flow is deflected off the shelf around the banks to continue north parallel to the shelf break (Fig. 11). Warm water intruding onto the shelf penetrates into the deeper areas on the landward side of the banks isolating a tongue of colder coastal water on top of the shallow banks (Fig. 7C, 7D, and 4). These dynamics are reflected in the plankton distribution on the shelf. Because biological productivity during the winter is low, plankton biomass acts as a quasi passive tracer, at least over time periods of a few days. Mesoscale fluctuations in the cross-shelf position of the Davidson Current are therefore likely to be reflected in the spatial distribution of chlorophyll and zooplankton. The quantitative link between hydrography and plankton concentration has been established. Figures 5 and 6 show that water low in chlorophyll and zooplankton penetrates farthest onto the shelf near transect 2 south of the shallow banks. This water is then found seaward of the banks parallel to the shelf break. Associated with the shallow banks is a tongue of water more similar in plankton concentration to coastal water, reflecting both the hydrography and bathymetry. This flow pattern is supported by previous winter current and dynamic height data given by Freeland et al. (1984) (see their fig. 5 and 6). Their dynamic height data show both the topographic deflection of the flow off the shelf at the southern edge of the bank and the concentration of flow on the seaward edge of La Perouse Bank. Sundby (1984) presented evidence of a similar isolation of cold, relatively fresh coastal water on top of shallow banks by a northward flowing current off the Norwegian coast.

The winter data invite comparison with summer conditions of the same area given by Mackas et al. (1980) and Denman et al. (1981). Summer plankton distributions are primarily a function of nutrient input from Juan de Fuca Strait and upwelling. Winter distributions seem to be primarily a function of the relative position of the two dominant water types on the shelf. A significant similarity in both the summer and winter plankton distributions is the suggested strong influence of topography, either directly by controlling advective processes or indirectly by initiating upwelling and vertical mixing. Summer zones of increased zooplankton and chlorophyll concentration over nearshore shallow banks were also present in winter. However, high zooplankton biomass near the outer edge of the shelf, and high chlorophyll concentrations on the outer edge of La Perouse Bank, observed during the summer, were not present in our winter data. Instead, the winter spatial distribution was dominated by a zone of increased biomass coincident with the hydrographic front, and a tongue of increased biomass over La Perouse Bank continuous with the nearshore area of high biomass. During both seasons, runoff along the coast results in a salinity gradient separating nearshore water from water on the outer edge of the continental shelf. The 32.00 isohaline marks the approximate outer limit of coastal water during both seasons. In the southern portion of the study area during the winter, the frontal gradient is both steeper (a change of 1.0 over 5 km opposed to 0.5 over the

same distance in summer) and coincident with a strong thermal gradient. Although nitrates are not limiting in either season, winter concentrations are on average twice that observed during the summer, reflecting both the difference in utilization due to low winter productivity and increased replenishment by the vertical mixing of winter storms. Concentrations of both phytoplankton and zooplankton over the shelf during the winter are on average an order of magnitude less than those found during the summer. Zooplankton peaks of 40 000 $\cdot m^{-3}$ over Swiftsure Bank in the summer (Mackas et al. 1980) are reduced to 4000 $\cdot m^{-3}$ in the winter. The lowest summer chlorophyll concentrations of 1 mg $\cdot m^{-3}$ are significantly larger than the 0.1 mg $\cdot m^{-3}$ concentrations seen in winter. Relative differences between areas of high and low biomass during both seasons were approximately 1 order of magnitude.

An effective use of infrared satellite imagery is in extending the temporal continuity of in situ data, which, by the nature of sampling, must be separated in time. As Platt (1978) stated, we cannot ignore temporal changes when conducting studies in the spatial domain. It is impossible to separate either time or space as the single independent variable. The use of synoptic scale satellite imagery at an appropriate sampling frequency, however, allows an otherwise unattainable approximation. Previous studies have shown that a time series of images can be used to both map advection and measure its rate (Brown et al. 1983; Ikeda and Emery 1984; La Violette 1984).

A visual inspection of the sequence of images recorded for this study showed that only small-scale thermal features (scales on the order of 5 km and less) varied in space over the time period of the study. This variability was primarily within the Coastal Current and probably reflects the greater influence of tidal advection and mixing on the thermal regime in shallow waters and near the mouth of Juan de Fuca Strait. The position of larger scale features, including the main frontal zone between the Coastal Current and the Davidson Current, mesoscale features within the Davidson Current, and the cold water over La Perouse Bank remained relatively constant over the week-long study period. We are therefore justified in presenting only one infrared image as being representative of thermal features at the spatial scales with which we are dealing. Most importantly, the imagery provides synoptic, quantitative justification for contouring the transects of in situ hydrographic data, which were temporally separated in sampling by as much as 4 d and spatially separated by 18.5 km. Low winter rates of biological activity and the strong spatial similarities between the imagery and biological patterns allow greater confidence in contouring and interpreting both the chlorophyll and the zooplankton distributions.

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References

ARMSTRONG, F. A. J., C. R. STEARNS, AND J. D. H. STRICKLAND. 1967. The measurement of upwelling and subsequent biological processes by means of the Technicon Autoanalyser and associated equipment. Deep-Sea Res. 14: 381–389.

BROWN, O. B., D. B. OLSON, J. W. BROWN, AND R. H. EVANS. 1983. Satellite infrared observation of the kinematics of a warm core ring. Aust. J. Mar. Freshwater Res. 34: 535–545.

CANNON, G. A., N. P. LAIRD, AND T. V. RYAN. 1975. Flow along the continental slope off Washington, Autumn, 1971. J. Mar. Res. 33: 97–107.

DENMAN, K. L., D. L. MACKAS, H. J. FREELAND, M. J. AUSTIN, AND S. H. HILL. 1981. Persistent upwelling and mesoscale zones of high productivity off the west coast of Vancouver Island, Canada. *In* F. A. Richards [ed.] Coastal upwelling. American Geophysical Union, Washington, DC.

DODIMEAD, A. J., AND A. BALLANTYNE. 1980. Oceanographic observations during fisheries research surveys off the British Columbia coast in 1979. Can. Data Rep. Fish. Aquat. Sci. 210.

DOUGLAS, M. L., AND W. P. WICKETT. 1978. Temperature conditions on the shelf off Barkley Sound, Vancouver Island, Feb. 28 – Mar. 9, 1978. Fish. Mar. Serv. Rep. 1492.

EMERY, W. J., AND K. HAMILTON. 1985. Atmospheric forcing of interannual variability in the northeast Pacific Ocean; connections with El Niño. J. Geophys. Res. 90: 857–868.

FOURNIER, R. O., M. VAN DET, J. S. WILSON, AND N. B. HARGREAVES. 1979. Influence of the shelf break front off Nova Scotia on phytoplankton standing stock in winter. J. Fish. Res. Board Can. 36: 1228–1237.

FREELAND, H. J., W. R. CRAWFORD, AND R. E. THOMSON. 1984. Currents along the Pacific coast of Canada. Atmos.-Ocean 22: 151–172.

FREELAND, H. J., AND K. L. DENMAN. 1982. A topographically controlled upwelling center off southern Vancouver Island. J. Mar. Res. 40: 1069–1093.

HAGER, S. W., L. I. GORDON, AND P. K. PARK. 1968. A practical manual for the use of Technicon Autoanalyser in seawater nutrient analysis. A final report to B.C.F. No. 14-17-0001-1759, Oct. 1968. Ref. 68-33.

HICKEY, B. M. 1979. The California Current System — hypothesis and facts. Prog. Oceanogr. 8: 191–279.

IKEDA, M., AND W. J. EMERY. 1984. A continental shelf upwelling event off Vancouver Island as revealed by satellite infrared imagery. J. Mar. Res. 42: 303–317.

IKEDA, M., W. J. EMERY, AND L. A. MYSAK. 1984. Seasonal variability in meanders of the California Current System off Vancouver Island. J. Geophys. Res. 89: 3487–3505.

LA VIOLETTE, P. E. 1984. The advection of submesoscale thermal features in the Alboran Sea Gyre. J. Phys. Oceanogr. 14: 550–565.

LEWIS, A. G. 1978. Concentrations of nutrients and chlorophyll on a cross-channel transect in Juan de Fuca Strait, British Columbia. J. Fish. Res. Board Can. 35: 305–314.

MACISAAC, J. J., AND R. C. DUGDALE. 1969. The kinetics of nitrate and ammonia uptake by natural populations of marine phytoplankton. Deep-Sea Res. 16: 45–57.

MACKAS, D. L., G. C. LOUTTIT, AND M. J. AUSTIN. 1980. Spatial distribution of zooplankton and phytoplankton in British Columbia coastal waters. Can. J. Fish. Aquat. Sci. 37: 1476–1487.

MACKAS, D. L., AND H. A. SEFTON. 1982. Plankton species assemblages off southern Vancouver Island: geographic pattern and temporal variability. J. Mar. Res. 40: 1173–1200.

PLATT, T. 1978. Spectral analysis of spatial structure in phytoplankton populations. *In* J. H. Steele [ed.] Spatial pattern in plankton communities. Plenum Press, New York, NY.

SIMPSON, J. J. 1983. Large scale thermal anomalies in the California Current during the 1982–1983 El Niño. Geophys. Res. Lett. 10: 937–940.

STEFANSSON, V., AND F. S. RICHARDS. 1963. Processes contributing to the nutrient distribution off the Columbia River and the Strait of Juan de Fuca. Limnol. Oceanogr. 8: 394–410.

SUNDBY, S. 1984. Influence of bottom topography on the circulation at the continental shelf off northern Norway. Fiskeridir. Skr. Ser. Havunders. 17: 501–519.

Carbon Flow in a Tundra Stream Ecosystem

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Peterson, B. J., J. E. Hobbie, and T. L. Corliss. 1986. Carbon flow in a tundra stream ecosystem. Can. J. Fish. Aquat. Sci. 43: 1259–1270.

The carbon cycle of the Kuparuk River, a meandering tundra stream, is dominated by inputs of eroding peat and leaching dissolved organic carbon from the tundra. Net production of epilithic algae is about 13 g $C \cdot m^{-2} \cdot yr^{-1}$, an order of magnitude less than inputs of allochthonous particulate organic carbon and two orders of magnitude less than inputs of dissolved organic carbon. The streamwater has a mean total organic carbon concentration of 6.8 $mg \cdot L^{-1}$, and the annual export of organic carbon from the watershed is 2–3 $t \cdot km^{-2} \cdot yr^{-1}$; both are similar to the average for temperate streams. However, because of the low primary productivity of tundra vegetation, the export of organic carbon from the watershed via the river is a larger fraction (2–6%) of the total watershed net primary production than the 0.1–0.4% usually found for temperate rivers.

Le cycle du carbone de la rivière Kuparuk, cours d'eau à méandres de la toundra, est surtout alimenté par le produit de l'érosion de la tourbe et le carbone organique dissous de lessivage provenant de la toundra. La production nette d'algues épilithiques est d'environ 13 $g \cdot m^{-2} \cdot an^{-1}$ de C, un volume inférieur d'une décimale aux apports de carbone organique particulaire allochtone et inférieur de 2 décimales aux apports de carbone organique dissous. L'eau du cours d'eau a une concentration totale moyenne de carbone organique de 6,8 $mg \cdot L^{-1}$ et le volume annuel de carbone organique charrié par le bassin hydrographique est de 2–3 $t \cdot km^{-2} \cdot an^{-1}$, ces deux valeurs étant analogues à la moyenne des cours d'eau tempérés. Cependant, en raison de la faible productivité primaire de la végétation de la toundra, le transport de carbone organique du bassin hydrographique par la rivière constitue une part plus importante (de 2 à 6 %) de la production primaire nette totale du bassin hydrographique que les 0,1 à 0,4 % habituellement enregistrés dans les rivières tempérées.

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The development of models of how streams function has been largely based on studies of temperate woodland streams. Carbon flow in these temperate streams is often dominated by allochthonous organic matter from terrestrial plants (Fisher and Likens 1973; Fisher and Carpenter 1976). But Vannote et al. (1980) described how these sources of organic carbon change as lower order streams increase in size downstream and heterotrophy gives way to autotrophy as the canopy of vegetation opens. Still it appears that Minshall (1978) is correct in his argument that autochthonous carbon production is important in many streams and rivers of all sizes. There have been no intensive studies of tundra streams and it is not known if such streams are similar in function to temperate and boreal streams.

We studied a section of the Kuparuk River on the North Slope of Alaska. Since there are no glaciers in the watershed and little springwater input, the Kuparuk is a clear water tundra stream by the classification of Craig and McCart (1975). They found that the North Slope tundra streams have intermediate levels of productivity, while glacier-fed streams have low productivity and spring-fed streams have high productivity (Craig and McCart 1975). We chose the Kuparuk, since it was both close to field laboratory facilities and has no large lakes in the watershed. In addition, there are no humans living in the watershed and no human disturbance except for light fishing near the trans-Alaska pipeline crossing.

The objective of our research was to examine in detail the standing stocks and fluxes of organic carbon in this tundra stream. This information can then be compared and contrasted with studies of temperate and boreal rivers. This knowledge of the carbon cycle of the Kuparuk River is serving as a basis for experiments designed to provide information on the controls of productivity and energy flow in the river. This information is needed to understand the possible changes that may occur due to future human disturbance.

The Kuparuk River

The river originates in the foothills of the Brooks Range and flows north–northeast to the Arctic Ocean (total drainage area of 8107 km^2). The section of the drainage basin we studied (Fig. 1) stretches from the headwaters of the Kuparuk River in the foothills of the Brooks Range to the river intersection with the Yukon River – Prudhoe Bay haul road. This area of 143 km^2 comprises the southernmost 1.8% of the total Kuparuk River drainage. The average channel slope over this stretch is 3.13% and the channel length is 24 km. At its intersection with the haul road, the Kuparuk River is fourth-order stream according to the classification of Dunne and Leopold (1978). The main stem of the Kuparuk in the 15 km immediately upstream

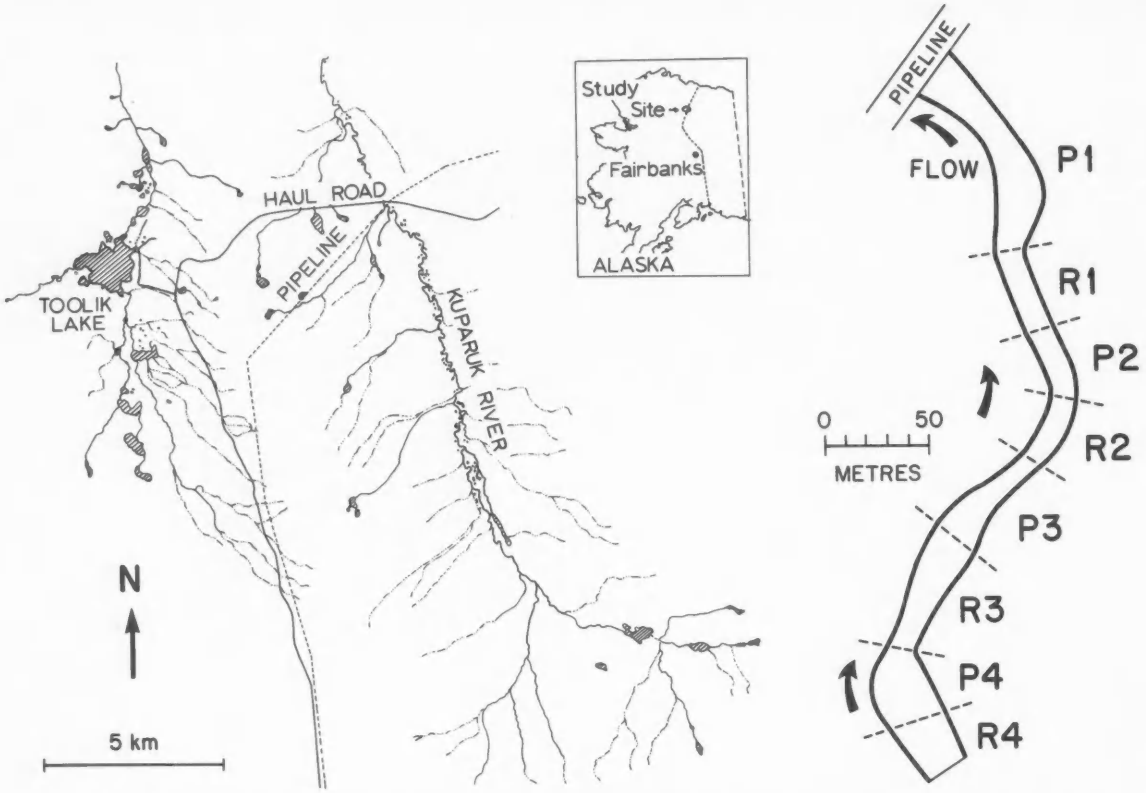

FIG. 1. Inset: location of the study site on the North Slope of Alaska. Left: upper Kuparuk River watershed from the foothills of the Brooks Range to the pipeline. Right: study reach consisting of four pools and four riffles upstream of the pipeline crossing.

of the haul road has a meandering channel with a sinuosity of 1.5 (Leopold et al. 1964). This meandering is important for the ecology of the river because peat eroding from the stream banks is the major input of particulate organic matter.

We have monitored the flow, water nutrient chemistry, and organic carbon concentrations for the upper Kuparuk River watershed for 1978, 1979, and 1980 (Peterson et al. 1983; Hobbie et al. 1983). Measurements were taken during most of the open-water season which extends from the beginning of flow in mid-May through September (flow ceases in late September). During the remainder of the year the Kuparuk is frozen solid. The discharge of the upper Kuparuk ranges from 0.1 to 30 $m^3 \cdot s^{-1}$ with a peak due to snowmelt in late May or June. Summer flows in the study years ranged from extremely high flow caused by heavy summer precipitation to low flows due to lack of precipitation.

Methods

Water flow was measured with a Gurley pigmy current meter during low flow and with the rhodamine dye dilution technique during high flows (>5 $m^3 \cdot s^{-1}$). After the discharge–height relationship was known, we measured stream stage at the site where the haul road crosses the river and calculated discharge.

Samples for dissolved inorganic carbon (DIC), dissolved organic carbon (DOC), and particulate organic carbon (POC) were collected in a rinsed 4-L plastic carboy. DIC concentration was calculated from the results of an alkalinity titration with 0.02 *M* HCl and a pH measurement (APHA 1975). Samples for DOC were first filtered through a Whatman GF/C filter which had been rinsed and preignited, and then the water samples (filtrates) were frozen for later measurement of DOC after wet chemical oxidation (Menzel and Vaccaro 1964). POC was determined by dry combusion of the material collected on the GF/C filters and measurement of the CO_2 evolved with a LIRA CO_2 analyzer.

Drift nets sampled both insects and large particulate organic carbon (LPOC is > 300 μm) in the water. All of the drift net material was preserved in formalin; later, half was picked for insects and the other half rinsed, dried at 60°C, weighed, and ashed for ash-free dry weight determination. Carbon was assumed to be 50% of the weight loss on ignition at 500°C.

The annual exports of DIC, DOC, POC, and LPOC were calculated based on measurements taken every 1–4 d from snowmelt in May to mid-August. Each day was assigned a mean value for flow based on either direct measurement or stage height and a mean value for each carbon species. Flow and carbon concentrations for days falling between measurements were estimated by linear interpolation. Samples were also taken at high flows due to either spring runoff or summer rains. Daily export was calculated by multiplying the daily discharge by the daily carbon concentration. The daily

export values were summed to give the seasonal export. A portion of each year's discharge was missed because we did not sample during late August and September. The percentage missed was computed on the basis of daily discharge for the entire year measured by the U.S. Geological Survey (1980) at the mouth of the Kuparuk. The carbon export values were adjusted linearly for the 2, 13, and 24% of the water years missed in 1978, 1979, and 1980, respectively.

All of the carbon stock and rate measurements were performed in a series of four pools and four riffles upstream (south) of the trans-Alaska pipeline crossing (Fig. 1). Chlorophyll on stream bottom rocks was sampled by two methods. In one method, an electric toothbrush with the brush remounted perpendicular to the shaft was used to scrub the rock surface inside a Plexiglas cylinder with a watertight rubber collar. In the second method, used on rocks incubated for photosynthesis and respiration measurements, the entire upper surface of the rock was scrubbed with a plastic bristle scrub brush. For measurement of the chlorophyll, a subsample of the water containing the particulate material dislodged from the rocks was filtered onto a Whatman GF/C glass fiber filter. The filters were then extracted in 90% acetone and the fluorescence was measured on a Turner flurometer. Fluorescence was converted to chlorophyll *a* by calibration based on spectrophotometer readings (Strickland and Parsons 1965).

Fine particulate organic carbon (FPOC) on and in the river bottom was collected in a 30-cm-diameter cylinder with a sponge rubber collar placed on the stream bottom. Rocks inside the cylinder were scrubbed and gravel down to a depth of 10 cm was stirred vigorously to resuspend the organic matter. A subsample of the water inside the cylinder was quickly taken and samples were filtered onto precombusted Whatman GF/C glass fiber filters, dried, and weighed before and after ashing.

LPOC and insects on the river bottom were collected with a Surber sampler with 300-μm mesh. As with the drift samples, these samples were split for LPOC and invertebrate counts. The samples were fixed with formalin (10% formaldehyde by volume) and later rinsed, dried, and ashed. We assumed that carbon was 40% of the organic matter as measured by combusting the sample. The insect identifications were made by Dr. Todd Harris (Purdue University, West Lafayette, IN).

Very large particulate organic carbon (VLPOC) was collected by hand from pools and riffles upstream of the road and pipeline crossings. These samples contained stems and twigs from the streamside dwarf birches (*Betula nana*) and willows (*Salix* sp.) but consisted mostly of chunks of peat ranging from fist-size pieces to chunks that were too large to move. The carbon content of the VLPOC was calculated from the volume of peat and wood. The organic matter content per unit volume of representative subsamples of both wood and peat was measured by ashing and weighing.

The rate of litter input to the stream was measured with open-top boxes with screen bottoms. Over the course of a field season (June–August) the boxes collected negligible amounts of litter, and we concluded that minor amounts of material enter the stream as litter except during high flow when the river captures material by flooding the banks.

Erosion of large amounts of peat from the river banks also occurs at high flow. The rate of erosion was measured each year from permanent stakes near the stream banks at points where there was active undercutting and bank slumping. A second assessment of the long-term average rate of peat erosion was obtained by measuring the organic carbon content of soil

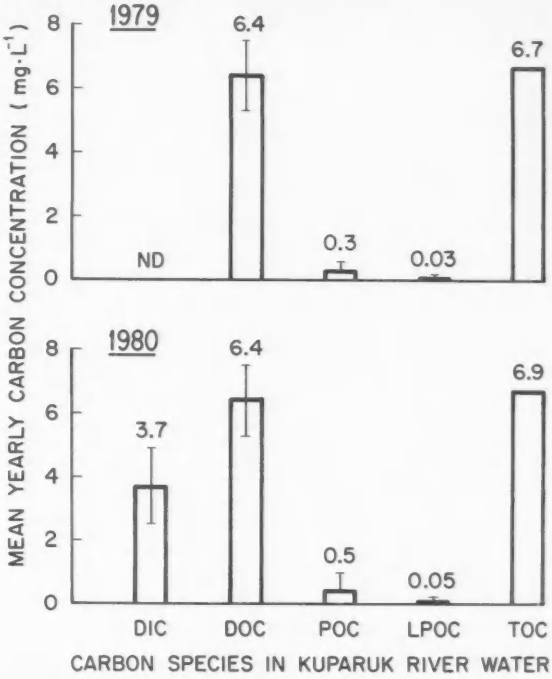

FIG. 2. Mean carbon concentrations in Kuparuk River water in the open-water seasons of 1979 and 1980. The error bars include ± 1 SD. The number of samples is 14 for DOC, 26 for POC, and 27 for LPOC during 1979 and 35 for DOC, 35 for POC, and 32 for LPOC during 1980.

profiles to 60 cm depth along two transects across the 400-m-wide flat bottom of the river valley, by measuring the ^{14}C age of the organic matter, and by making the assumption that the average annual input was equal to the total carbon in the transect divided by the ^{14}C age at the bottom of a profile. Samples from the bottom of the deepest peat profiles on the river bank just above the mineral soil were analyzed for ^{14}C age by Krueger Enterprises, Inc., Cambridge, MA.

The rates of decomposition of common grasses, dwarf tree leaves, and peat were determined using litter bags tethered with monofilament to stakes driven into the river bottom at both pool and riffle sites. The litter bags were constructed of fiberglass screen with 300-μm mesh size. After incubation in the stream, the material inside was weighed before and after ignition. Carbon was assumed to be 40% of the weight loss on ignition.

The metabolism of the epilithon community on the river bottom was measured by monitoring changes in dissolved oxygen in light and dark Plexiglas chambers. The chambers were filled with rocks from the river bottom and with river water. Water was circulated in the chambers with submersible pumps powered by a portable generator. Oxygen was determined by Winkler titration of water samples withdrawn from the chambers at $t = 0$ and $t = 4$ or more hours depending on rates of O_2 change.

The ratio of ^{13}C to ^{12}C in the major sources of organic matter and in insects and grayling (*Thymallus arcticus*) was measured to assess this ratio as a food web tracer. Samples were collected and dried in the field and analyses were run by W. Deuser, Woods Hole Oceanographic Institution, Woods Hole, MA.

TABLE 1. Linear regression analysis of carbon concentrations versus flow ($m^3 \cdot s^{-1}$) for 1978, 1979, 1980, and for the years combined. The general equation is $y = mx + b$ where y is the concentration of the various forms of carbon, x is the flow, m is the slope of the line, and b is the intersect.

Years	Carbon form y	Slope m	Intercept b	n	r
1979	DOC ($mg \cdot L^{-1}$)	0.11	+5.6	14	+0.73
1980		0.17	+5.5	35	+0.62
1979, 1980 (combined)		0.15	+5.6	49	+0.62
1978	POC ($\mu g \cdot L^{-1}$)	51.00	+79.0	16	+0.62
1979		36.00	+8.5	26	+0.78
1980		66.00	+136.0	35	+0.73
1978, 1979, 1980 (combined)		54.00	+97.0	77	+0.68
1979	LPOC ($\mu g \cdot L^{-1}$)	6.90	−3.3	27	+0.69
1980		10.10	−2.7	32	+0.48
1979, 1980 (combined)		9.10	−4.8	59	+0.50
1978, 1980 (combined)	DIC $mg \cdot L^{-1}$)[a]	0.45	+1.8	25	+0.79

[a]The last regression relates DIC concentration in the river water (y) to the number of days (x) since iceout until the sample was taken.

Results

Carbon Concentrations and Export

Carbon is exported from the watershed via the river as DIC, DOC, POC, and LPOC (Fig. 2); concentrations of DOC were usually greater than DIC and much greater than POC. The POC concentrations were in turn an order of magnitude higher than LPOC concentrations. Of the POC, less than 15% was living bacteria and algae. The bacterial biomass was calculated from direct counts of bacteria in the river water (Hobbie et al. 1983) converted to carbon (bacteria contain 1×10^{-14} g $C \cdot cell^{-1}$). We found that bacteria made up a small percentage of the POC, about 5 ± 3% on average. A series of measurements of chlorophyll *a* in river water from May through August 1978 gave values ranging from 0.09 to 1.61 μg Chl $a \cdot L^{-1}$ with a mean value of 0.44 ± 0.34 (n = 17) (Jeff Cornwell, Institute of Marine Science, University of Alaska, Fairbanks, AK). Assuming a C:Chl ratio of 50:1 by weight (Strickland 1960), the algae comprised less than 10% of the POC which averaged 300−500 μg $C \cdot L^{-1}$.

The concentration of DIC in the water increased as the season progressed, perhaps because water comes from deeper in the soils as the frozen ground melts, and this water carries more respiratory CO_2 (Table 1). The result is that the regression of DIC versus day of the year (n = 25, r = +0.79) produces a much stronger correlation than regression of DIC versus flow (r = 0.44, not shown). River discharge has a definite impact on the concentrations of the various forms of organic carbon in the water (Table 1). Concentrations of all forms of organic carbon increased with rising discharge. Summer DOC levels range from around 5 $mg \cdot L^{-1}$ at low flow up to 10 or 12 $mg \cdot L^{-1}$ at high flow. In 1978, we had only a few samples for DOC, but early in the year we found values of around 15−20 $mg \cdot L^{-1}$. Either these samples were contaminated or there was a pulse of high DOC that appeared early in the year which was not accompanied by high flow. In 1979 and 1980, we collected fewer samples in the early part of the season and we did not observe these high spring values. POC concentrations ranged from around 150 $\mu g \cdot L^{-1}$ at low flows to over 1000 $\mu g \cdot L^{-1}$ at high flow.

Our estimates of the export of carbon (kilograms carbon per square kilometre per year) from the watershed are as follows:

Year	DIC	DOC	POC	LPOC	Total organic C
1978	—	—	66	—	—
1979	—	1800	98	12	1910
1980	1538	2671	310	40	3021

These values include the spring runoff and the entire open-water season. The annual total organic carbon exports were 1.9 and 3.2 t $C \cdot km^{-2} \cdot yr^{-1}$ for 1979 and 1980, respectively. Most of this material must have been derived from the tundra, since the amounts of carbon exported were far higher than could be attributed to periphyton production in the river (see next section). The LPOC collected in the drift nets contained mostly what appeared to be shredded peat. This comes from the peat swept into the channel during the erosion of the stream bank (see next section). The total organic carbon export amounts to a small fraction of the annual productivity of the terrestrial vegetation in the watershed, about 2−6% if we assume a net aboveground production of 50−100 g $C \cdot m^{-2} \cdot yr^{-1}$ (G. Shaver, Marine Biological Laboratory, Woods Hole, MA, pers. comm.).

Carbon Stocks in the Study Section

We selected a series of four pools and four riffles immediately upstream of the pipeline crossing for intensive measurements of carbon stocks and transformations. The particulate carbon on the river bottom and in the surficial sediments was separated into FPOC, LPOC, and VLPOC. The FPOC size class was further subdivided into fines (150- to 335-μm size) and ultrafines (1- to 150-μm size). FPOC stocks were measured only once in mid-August 1979. There were roughly equal amounts of carbon in the fine and ultrafine categories but the stocks of FPOC in pools were much greater than the stocks in riffles (Table 2). In contrast with the distribution of fines and

TABLE 2. Benthic carbon stocks (g C·m^{-2} ± SD) in the Kuparuk River, Alaska.

Category by size	Site	Standing stock	N
Ultrafines (1−150 μm)	Pool	3.9 ± 2.3	8
	Riffle	0.6 ± 0.3	8
Fines (150−335 μm)	Pool	3.0 ± 2.1	8
	Riffle	0.1 ± 0.2	8
LPOC (>335 μm)	Pool	16.4 ± 6.7	8
	Riffle	12.1 ± 8.5	8
VLPOC (>10 cm)	Pools and riffles	10.0	Combined sample

ultrafines, LPOC was about equally distributed between pools and riffles and there was much more carbon in this category than in the fines. The VLPOC was extremely patchy in its distribution, so we combined the collections for the pool and riffle areas and obtained an overall mean value of 10 g C·m^{-2}. The patchy distribution appeared to be due mainly to the fact that large chunks of peat were more abundant near points where erosion was causing banks to slump and cave in. Subsequent dispersal probably requires breaking up the large chunks into the LPOC and FPOC size classes.

The standing stock of total POC (ultrafines, fines, LPOC, and VLPOC) on the river bottom was very large and totaled about 20−30 g C·m^{-2}. For comparison, the standing stocks of organic carbon as DOC, POC, and LPOC suspended in the water (0.5 m mean depth) were 3.2, 0.2, and 0.02 g C·m^{-2}, respectively.

The standing stocks of algae on the stream bottom rocks were estimated by means of chlorophyll determinations and converted to carbon units assuming a C:Chl weight ratio of 50:1 (Strickland 1960). On July 7−10, 1978, rocks in the study section showed values of 1.17 ± 1.93 mg Chl *a*·m^{-2} for riffles and 6.78 ± 3.19 for pools (N = 24). In 1980, values of 1.47 ± 0.60 (N = 12) and 3.36 ± 2.97 (N = 14) were found for riffles and pools, respectively. A grand average chlorophyll value combining both years and pools and riffles was 3.22 mg Chl *a*·m^{-2}, which converts to about 0.2 g C·m^{-2} in epilithic algae. The large standard deviations show that chlorophyll concentrations were quite variable. However, rocks on the bottom of pools had more chlorophyll than those in riffles. Current velocity in riffles ranged from 0.3 to 1.0 m·s^{-1} whereas in pools the velocity ranged from 0.05 to 0.4 m·s^{-1}. While chlorophyll levels are quite variable at any current velocity, there appeared to be a maximum level which is not exceeded at any given flow rate. However, in subsequent experiments when the stream was fertilizerd with phosphorus, the relationship between current velocity and chlorophyll was greatly altered and chlorophyll levels of up to 40 mg·m^{-2} were found on rocks in the riffles (Peterson et al. 1985).

Surber samples were taken during August 1979 to census the macroinvertebrates in the river. Mayflies dominated the collections in terms of biomass but chironomids dominated in terms of numbers. Mayfly species belonging to the genus *Baetis* and the mayflies *Ephemerella aurivilli* and *Cinygmula atlantica* scrape rock surfaces for periphyton and detritus, while *Metretropus norvegicus* is a predator. The chironomids were represented by eight genera in the August collections. A random sample of 100 chironomids included 35 predaceous chironomids and 65 collector−gatherers. Only two species of stonefly were collected, both in low numbers; *Nemoura trispinosa* is herbivorous and *Chloroperla ovibovis* feeds on either plant or animal material. All of the five species of blackflies (Simuliidae) possess cephalic fans for filtering particles carried by the water. Four species of Trichoptera (caddis flies) were collected in the Kuparuk and three additional species were collected as adults in sweep net samples near the river. The most abundant species was *Brachycentrus* nr *americana*, a filter feeder and grazer; 56 *B. americana* were collected in one Surber sample from a riffle. *Rhyacophila vofixa*, the only other common caddis fly, is a free-living predator.

TABLE 3. Carbon-14 and $\delta^{13}C$ values for basal peat and a grayling collected in August from the upper Kuparuk River.

Sample	^{14}C age or % modern	$\delta^{13}C$ (‰)
Pool 1, stake 4	2815 ± 120 yr B.P.	−28.1
Pool 1, stake 3	2400 ± 140 yr B.P.	−27.9
Pool 4, stake 7	1735 ± 125 yr B.P.	−28.8
Arctic grayling	120.4% modern (1950)	−28.5

We observed only one species of fish in the river during this study, the sailfin arctic grayling (*Thymallus arcticus signifer*). During the three years, we observed from two to five large grayling (30−40 cm) in each pool. This is equivalent to about 0.1 g C·m^{-2}, but this estimate may be low because of the difficulty of spotting these fish, especially in the riffles. No small fish were seen during 1978, 1979, and 1980. However, during 1983, large numbers of young grayling less than 8 cm were seen. It appears that recruitment of young fish is variable from year to year. During the late summer, grayling move upstream presumably to headwater lakes where they overwinter. In 1985, two specimens of arctic char (*Salvelinus alpinus*) were collected in the upper Kuparuk and numerous larval grayling were observed along the river near the road crossing.

Transformations of Carbon in the Study Site

There are many sites where the river is undermining its banks with a resulting erosion of peat. Cores of peat collected on two east−west transects of the flat valley bottom (~400 m wide) gave a mean of 11 610 kg organic C in the upper 60 cm of the 1-m-wide transects. The ^{14}C analyses of the basal peat indicated an average age of 2300 yr (Table 3). We interpreted the radiocarbon date to indicate that the total organic carbon stock in a transect is captured via stream channel migration in an average time of 2300 yr. The long-term mean capture rate is then 5 kg C·m^{-1}·yr^{-1}. Since the average bank to bank stream width in this reach is 17 m, the rate of capture of peat carbon is 300 g C·(m^2 of river bottom)$^{-1}$·yr^{-1}.

A second estimate of the rate of soil organic matter capture was obtained by direct measurement of the rate of bank ero-

TABLE 4. Photosynthesis and respiration of the epilithic community of the Kuparuk River (n = number of chambers used; R = riffle; P = pool; ND = not determined).

Date	Location	n	Chl a ($mg \cdot m^{-2}$)	Photosynthesis	Respiration	Net production
				(mg $C \cdot m^{-2} \cdot d^{-1}$)		
July 5, 1978	R	1	3.6	504	180	324
July 10, 1978	P	1	21.9	558	153	405
July 18, 1978	R	1	3.5	441	252	189
July 28, 1978	P	1	ND	243	162	81
July 23, 1980	P	4	6.5	351	114	223
July 28, 1980	R	3	1.9	25	6	18
August 11, 1980	P	3	1.2	46	16	30
August 12, 1980	R	4	1.3	47	12	34
August 18, 1980	P	2	2.1	41	18	18
Mean ± SD				250 ± 219	101 ± 91	147 ± 146

sion. To do this we surveyed 20 sites of potential erosion in three consecutive summers. In 14 of these locations there was measurable erosion over these two years. At five other sites the stream had undercut the banks causing slumping, but the top 30–50 cm of peat was still intact because of binding by plant roots. Using only the 14 eroded sites, we calculated the mean erosion as 0.26 ± 0.40 m in two years or 0.13 $m \cdot yr^{-1}$. From our measurements on cores we calculated a standing stock of carbon of 52 $kg \cdot m^{-2}$ in the upper 60 cm of the profile. This gives an estimate of carbon input of 6.8 $kg \cdot m^{-2} \cdot yr^{-1}$. Since the river is only eroding actively on half of its shoreline (the outer side of bends), this rate of carbon input is 200 $g \cdot m^{-2} \cdot yr^{-1}$. This is probably a conservative estimate, since we did not include any large but rare events such as oxbow lake formation, we assumed no organic matter below 60 cm in the soils, and we did not include inputs from the areas where only streambank slumping occurred. Nonetheless, the agreement between the direct erosion estimates and the long-term ^{14}C calculations is good considering that they cover such different time intervals.

There are large chunks of peat on the bottom of many pools in the river. We tagged two of these by tying rope around them in 1980. In 1983 one could not be found. Probably this one had either been buried under gravel and rocks during high flows or had broken up and washed downstream. During high flows (>20 $m^3 \cdot s^{-1}$) the entire bottom of the river can move, as we have observed that burlap sacks filled with rocks can move up to 10 m in a riffle during a single high water event. The second chunk was still on the bottom of the same pool and still had roughly the same dimensions as when it was tagged. By 1985 this second chunk had been moved about 20 m downstream and was approximately one-half its original size. We have also observed other large chunks that remained for several years in deep pools. The residence time of these large chunks can be very long compared with the rapid turnover of organic carbon in the FPOC and POC pools.

Photosynthesis and respiration of the epilithon are similar in pool and riffle areas (Table 4). Rates of photosynthesis and respiration were higher in 1978 than in 1980 with the exception of July 23, 1980. The most likely reason for this is that in 1980 there were three large storms during July and August which may have dislodged or scoured epilithon from the rocks. This conjecture is supported by the lower chlorophyll levels in 1980. In contrast, 1978 had no storms during July. Taking the grand mean of these 1978 and 1980 measurements, we find an average daily rate of gross photosynthesis of 250 mg $C \cdot m^{-2} \cdot d^{-1}$, net production of 147 mg $C \cdot m^{-2} \cdot d^{-1}$, and respiration of 101 mg $C \cdot m^{-2} \cdot d^{-1}$. Taking half of June, all of July and August, and half of September as the productive period gives an annual estimate of gross production of 22 g $C \cdot m^{-2} \cdot yr^{-1}$ and net production of 13 g $C \cdot m^{-2} \cdot yr^{-1}$. This level of production is similar to the phytoplankton production in nearby Toolik Lake of 15 g $C \cdot m^{-2} \cdot yr^{-1}$ as measured by ^{14}C-CO_2 uptake (M. Miller, University of Cincinnati, Cincinnati, OH). Comparing the rate of peat input to the river with the rate of epilithiphyton production shows the strong predominance of allochthonous carbon inputs (200–300 g $C \cdot m^{-2} \cdot yr^{-1}$) over autochthonous net production (13 g $C \cdot m^{-2} \cdot yr^{-1}$).

Litter enters the stream as stems, leaves, and grass blades from the vegetation near the river but we were unable to measure these inputs with litter traps. Litter is prevented from blowing into the stream by the tussock tundra and by the dwarf (1 m tall) trees along the banks, but during high flows the river does capture litter from the streamside. Once in the stream, litter must be decomposed before it can be used as food by aquatic insects. The rates of decomposition of leaves, grasses, and peat, measured in litterbags (Table 5), revealed large differences in rates between pools and riffles. Decomposition in riffles is much faster than in pools and this is probably indirectly related to the increased water turbulence and velocity in riffles. Despite this difference in disappearance rates, there is almost as much LPOC in riffles as in pools (Table 2). However, the fines are concentrated in pools.

It is difficult to compare the rates of decomposition measured over the 10-wk summer with rates for an entire year because most litterbags left to overwinter in the stream were lost in the high water of the spring runoff. For those litter types where we do have data after 1 yr, much more organic matter remained than predicted by extrapolating the rate of litter decomposition measured during the summer (Table 5). For example, the regression of weight versus time for *Betula nana* leaves in pools predicts only 12.5% remaining at 52 wk, whereas we measured 38%. The differences are due to the fact that the river is frozen from October to May. There were also large differences in decomposition rates between species; *Eriophorum vaginatum* and *Betula nana* had the highest rates of decomposition, *Carex aquatilus* and *Salix* sp. had intermediate rates, and peat had the lowest rate of decomposition. In fact, peat decomposition is probably overestimated in these experiments because peat tends to fragment easily and the fine particles which may es-

TABLE 5. Rates of decomposition of leaves of the dominant tundra plants and peat in pools and riffles of the Kuparuk River (N = number of litterbags which contributed data for the regressions; NS = not statistically significant at the 0.05 level).

Species	Location	Decay rate ($k \cdot wk^{-1}$)	Correlation coefficient	N	Measured percent remaining after 1 yr
Betula nana	Pool	−0.039	−0.93	15	38
	Riffle	−0.123	−0.95	13	
Carex aquatilus	Pool	−0.030	−0.70	13	38
	Riffle	−0.033	−0.41 (NS)	12	
Salix sp.	Pool	−0.029	−0.86	13	57
	Riffle	−0.045	−0.93	13	
Eriophorum vaginatum	Pool	−0.043	−0.91	14	29
	Riffle	−0.120	−0.96	13	
Peat	Pool	−0.007	−0.96	6	66

[a]These decay rates were determined by the rate of organic matter loss from litterbags over 10 wk during June, July, and August except for peat which was measured over 52 wk because of its slow rate of decay.

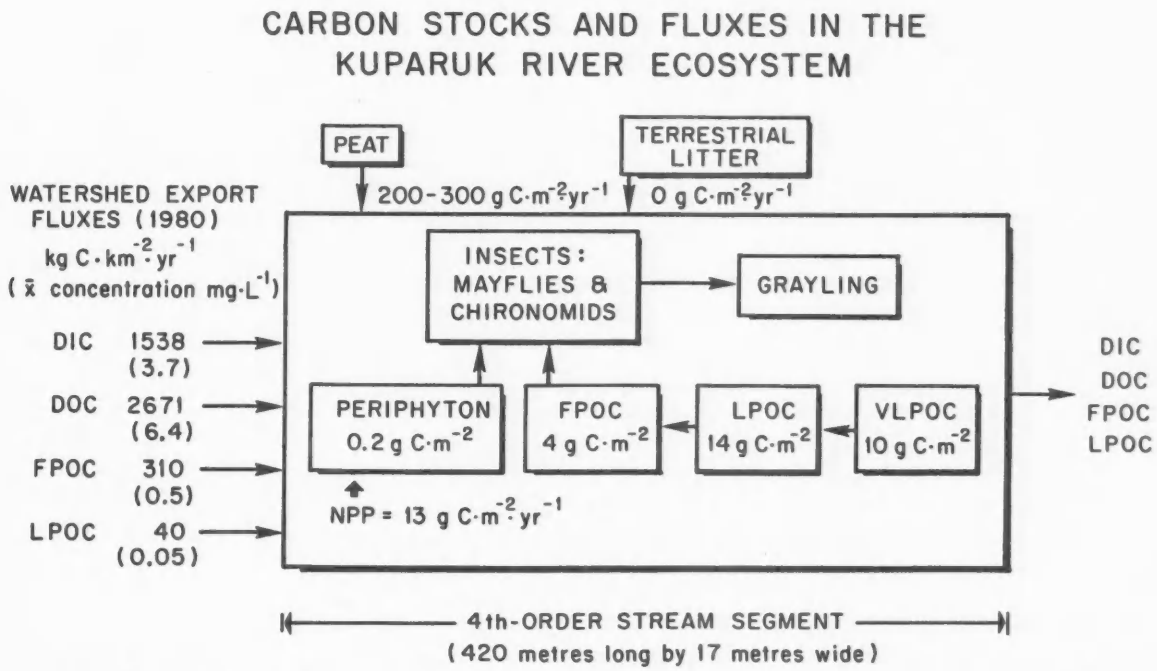

FIG. 3. Carbon stocks and fluxes for the Kuparuk River watershed upstream of the trans-Alaska pipeline. NPP is net primary production of epilithiphyton.

cape the litterbag are very likely still refractory and not decomposed.

We did a survey of the $\delta^{13}C$ values (the difference from a standard ratio of $^{13}C:^{12}C$) of plants and animals of the Kuparuk River to determine if these values would provide evidence about the transfer of carbon in the food web in the river. The results were discouraging, since the $\delta^{13}C$ values for terrestrial plants ranged from −26.0 to −27.3‰ whereas epilithon which grew on Plexiglas plates in the river had a $\delta^{13}C$ value of −27.2‰. Peat also had almost the same ^{13}C content as epilithon (−27.1‰). Therefore, we could not distinguish the relative contributions of land plants, peat, and algae to detritus or to other organisms by using $\delta^{13}C$ values. Yet, there were differences among consumers as shown by different species of aquatic insects which ranged from −25.7 to −32.3‰. This is a wide range but it is not apparent what causes this variation. The three adult grayling sampled had $\delta^{13}C$ values ranging from −23.4 to −28.5‰. The tendency for some insects and fish to have higher $\delta^{13}C$ values than the plants may be due to metabolic fractionation, as has been observed by Rau et al. (1983) and McConnaughey and McRoy (1979). Confronted with this variation in ratios at the higher trophic levels at the same time that there were only very small differences among the potential organic matter sources, we conclude that the carbon isotope

TABLE 6. Mean annual gross primary production of rivers (modified from Minshall 1978 and Fisher and Carpenter 1976).

Name and location	Gross production ($g\ C \cdot m^{-2} \cdot d^{-1}$)	Reference
A. High productivity		
Tecopa Bore, CA	6.7	Naiman 1976
Rainbow Springs, FL	6.7	Odum 1957b
Silver Springs, FL	6.3	Odum 1957a
Skeleton Creek, OK	5.3	Prophet and Ransom 1974
Blue River, OK	1.1–8.2	Duffer and Dorris 1966
River Ivel, G.B.	3.5	Edwards and Owens 1962
Truckee R., NV	3.3	Thomas and O'Connell 1966
River Arakawa, Japan	2.4	Tominaga and Ichimura 1966
Deep Creek, ID	1.0–3.8	Minshall 1978
B. Intermediate productivity		
Buffalo Cr., PA	2.1	McDiffert et al. 1972
Madison R., CA	1.8	Wright and Mills 1967
Logan R., UT	1.3–1.7	McConnell and Sigler 1959
Rattlesnake Creek, WA	1.1	Cummings et al. 1983
New Hope Creek, NC	1.0–1.6	Hall 1972
Neuse River tributaries, NC	0.7	Hoskin 1959
Fort River, MA	0.7	Fisher and Carpenter 1976
Cone Spring, IA	0.7	Tilly 1968
C. Low productivity		
Root Spring, MA	0.22	Teal 1957
McKenzie River, OR	0.11–0.33	Naiman and Sedell 1980
Lookout Creek, OR	0.11–0.33	Naiman and Sedell 1980
Mack Creek, OR	0.08–0.22	Naiman and Sedell 1980
Moisie River, Que.	0.04–0.18	Naiman 1983
Berry Creek, OR	0.02–0.22	Warren et al. 1964
Muskrat River, Que.	0.02–0.21	Naiman 1983
Beaver River, Que.	0.02–0.14	Naiman 1983
Devils Club Creek, OR	0.03–0.08	Naiman and Sedell 1980
Kuparuk River, AK	*0.06*	*This study*
First Choice Creek, AK	0.02–0.06	Naiman 1983
Bear Brook, NH	0.003	Fisher and Likens 1973

ratios are not useful for tracing organic carbon flow from producers to consumers in this system.

A second means of tracing the flow of peat carbon is via ^{14}C dating, since the peat carbon entering the river has a mean age of 1150 yr (Table 3). A grayling taken from the study reach on August 4, 1980, had a ^{14}C activity of 120% of modern. Since the activity of modern terrestrial carbon is 123–127%, this may indicate that this grayling contained a small amount (10–15%) of peat carbon (Schell 1983). Additional samples covering the entire season would be needed to verify this estimate of peat use, since the ^{14}C activity difference is very small.

Discussion

A summary of the export of carbon from the watershed and the carbon stocks and flows in the 420-m study section of the Kuparuk River is presented in Fig. 3. About 92% of the total organic carbon export is composed of DOC. The remainder of the total organic carbon export is POC. FPOC is 7% and LPOC is 0.7% of the total organic carbon export. The lateral input of carbon from the tundra was mostly peat, as there was little movement of litter from the tundra surface; estimated input from bank erosion ranged from 200 to 300 $g\ C \cdot m^{-2} \cdot yr^{-1}$.

There is an additional way to calculate whether or not the magnitude of peat inputs is reasonable. The river has a meandering course for 15 km upstream of our study site whereas above that the smaller tributaries do not meander. If the river banks throughout this 15 km eroded at a rate comparable with that at our study site, 30 000–80 000 $kg\ C \cdot yr^{-1}$ would enter the river. This is not an unreasonable value because in 1980 we measured an export of FPOC alone of 50 000 $kg\ C \cdot yr^{-1}$. One implication of this is that a large proportion of this peat-derived carbon is exported unchanged; this is consistent with our decomposition experiments which indicated that two thirds of the peat remained even after a whole year of decomposition in litterbags (Table 5). As noted, most of this POC must be from allochthonous sources, since periphyton production calculated for the upstream reaches (assuming a 15-km reach of 12 m average width and 20 $g\ C \cdot m^{-2} \cdot yr^{-1}$ net production) would yield only 4500 kg FPOC. The same argument applies to DOC. Most of this must be leachate from the terrestrial vegetation and peat, since DOC export is ninefold greater than FPOC export and two orders of magnitude larger than autochthonous primary production.

The stocks of organic carbon on the river bottom were also dominated by detritus derived from peat and streamside vegetation. Stocks of VLPOC (10 $g\ C \cdot m^{-2}$) and LPOC (14 $g\ C \cdot m^{-2}$) were greater than FPOC (4 $g\ C \cdot m^{-2}$). The biomass of epilithic

TABLE 7. Chlorophyll *a* concentrations in the epilithon of rivers (adapted from Naiman and Sedell 1980).

River and location	Stream order	Concentration (mg Chl·m^{-2})	Comments	Reference
Logan River UT	5–7	250–350	95% CI	McConnell and Sigler 1959
White Clay Creek, PA	3	16–402	Summer, open meadow stream	Bott et al. 1978
Blue River, OK	8	20–390	Summer, low discharge	Duffer and Dorris 1966
Tecopa Bore, CA	2	20–280	Annual range	Naiman and Gerking 1975
Flynn Creek, OR	3	20–122	July–December	Lane 1965
Mack Creek, Que.	3	36–95	Seasonal range	Naiman and Sedell 1980
McKenzie River, Que.	7	31–90	Seasonal range	Naiman and Sedell 1980
Lookout Creek, Que.	5	18–96	Seasonal range	Naiman and Sedell 1980
Needle Branch, OR	2	20–80	July–December	Lane 1965
Devils Club Creek, Que.	1	19–48	Seasonal range	Naiman and Sedell 1980
Carnation Creek, B.C.	5	1–40	Mean annual concentration	Stockner and Shortreed 1976
Kuparuk River, AK	*4*	*1–22*	*Summer range*	*This study*
Otter Creek, OK	3	3–15	Winter–summer range	Seyfer and Wilhm 1977
Otter Creek, OK	4	2–6	Winter–summer range	Seyfer and Wilhm 1977
Otter Creek, OK	5	1–6	Winter–summer range	Seyfer and Wilhm 1977
Otter Creek, OK	6	0–3	Winter–summer range	Seyfer and Wilhm 1977

TABLE 8. Energy contributions (g C·m^{-2}·yr^{-1}) from endogenous (as net primary production) and exogenous (litter fall) sources (adapted from Minshall 1978).

River and Location	Autochthonous	Allochthonous	Reference
Bear Brook, NH	0.6	251	Fisher and Likens 1973
Kuparuk River, AK	*13*	*100–300*	*This study*
Root Spring, MA	73	261	Teal 1957
New Hope Creek, NC	73	238	Hall 1972
Fort River, MA	169	213	Fisher 1977
Cone Spring, IA	119	70	Tilly 1968
Deep Creek, ID 1	206	0.2	Minshall 1978
Deep Creek, ID 2	368	7	Minshall 1978
Deep Creek, ID 3	761	1.1	Minshall 1978
Thames River, England	667	16	Mann et al. 1970
Silver Springs, FL	981	54	Odum 1957a
Tecopa Bore, CA[a]	1229	0	Naiman 1976

[a]A thermal spring.

algae was 0.2 g C·m^{-2} and net primary production was variable from year to year but averaged about 13 g C·m^{-2}·yr^{-1}. The stream insects derive their food from algal production and allochthonous carbon inputs made available through bacterial processing of peat and litter. The grayling feed on the aquatic insects.

The residence time of the average gram of detrital POC on the river bottom must be rather short if our estimates of fluxes and standing stocks are accurate. The standing stock on the river bottom amounts to about 30 g C·m^{-2} whereas about 250 g C·m^{-2}·yr^{-1} is added by erosion of the stream banks. Thus, the residence time is only 0.1–0.2 yr for an average gram of POC. Possible fates include breakup and export downstream, microbial degradation and respiration, or burial in the stream bottom below the 10-cm depth of sampling. We think most is exported either as fine particles or as DOC.

There are large differences in organic carbon export from year to year, a result of differences in flow regimes. For example, the total annual export of POC in 1980 was fivefold greater than the export in 1978. Flow in 1978 was never greater than 12 m^3·s^{-1}, whereas there were three storms with discharge greater than 20 m^3·s^{-1} in 1980. While the discharge is clearly related to the export of POC, the relationship is not proportional. For example, on July 14, 1980, flow was 25 m^3·s^{-1}, while export of POC was 87 000 mg C·s^{-1}. One week later, flow was 0.5 m^3·s^{-1}, while export was 60 mg C·s^{-1}. This 1500-fold difference in export is due to both flow changes (50-fold) and the change in POC concentration which increases as discharge rises (Table 1). The 1979 POC export was between the 1978 and 1980 values, probably because 1979 had three high discharge events with flow greater than 15 m^3·s^{-1}. Variations in stream flow from year to year probably result in differences in the input, fragmentation and decomposition, and export downriver of the peat. Perhaps peat remains on the river bottom during low-flow years but is exported during high flow in subsequent years. Perhaps the high POC export in 1980 included peat which was in the river the previous year(s) but was not exported. Much of this holdover peat storage probably is in the form of large chunks (VLPOC), as our observations have shown that large chunks can persist for several years.

Our studies show that net primary production is very low in the Kuparuk (13 g C·m^{-2}·yr^{-1}). Similar low rates are often found in forested temperate streams of similar size where normally light is limiting. However, there is no forest canopy over the Kuparuk, so we designed an experiment to find out if nutrients were limiting (Peterson et al. 1983). During July and August 1980, we ran two nutrient enrichment bioassays in continuous-flow tubes enriched with phosphorus and nitrogen.

Phosphate increased epilithiphyton biomass and ^{14}C-CO_2 uptake by 3- to 10-fold. Nitrogen alone gave no increase in biomass or activity. Even with nutrient enrichment, however, autochthonous production would still be more than an order of magnitude less than inputs of carbon as eroding peat and DOC.

It appears that gross primary production in the Kuparuk is among the lowest reported for a river (Table 6). The mean annual gross primary productivity of most springs, streams, and rivers range from 10- to 100-fold greater. Most of the other streams in the low-productivity category are in temperate and boreal forests where light is limiting because of shading by forest canopies. The phosphorus limitation in the Kuparuk has already been mentioned; one additional reason for the low annual production is that the open-water growing season in the Arctic is short, usually about 4 mo. Also, even during the open-water season, the spring runoff and later high flow events may keep production low by repeatedly scouring the rock surfaces and removing the epilithon. A comparison of chlorophyll *a* levels of epilithon in a variety of streams also suggests that the Kuparuk is among the least productive streams studied (Table 7).

There appears to be a reciprocal relationship between autochthonous and allochthonous carbon sources in streams (Table 8). Small woodland streams and springs obtain the bulk of their energy from allochthonous sources, whereas the metabolism of desert streams and larger rivers often results almost entirely from autochthonous primary production. From these ratios, the Kuparuk River would appear to be similar to small woodland streams and springs. Yet this ratio of the sources of organic carbon may give little information on the source of metabolizable carbon for the Kuparuk, since the DOC and peat are likely very refractory. As noted in Table 5, peat decays much slower than leaves of the tundra plants. These studies have not answered the questions about utilization of these materials as sources of energy, and it is still possible that the slow decomposition of a large amount of peat may provide more metabolizable organic carbon for consumers than the very low in situ primary production (Peterson et al. 1985).

How does the Kuparuk compare with other streams with respect to organic carbon concentrations and export? There are very few studies of tundra streams: Meybeck (1981) listed only five and these had average total organic carbon concentrations ranging from 1.5 to 5.4 $mg \cdot L^{-1}$. The Kuparuk had mean annual total organic carbon concentrations of 6.7 and 6.9 mg $C \cdot L^{-1}$ for 1979 and 1980, respectively. Figure 4A shows that the Kuparuk falls in the middle of the list of more than 100 rivers from all biomes in terms of mean annual concentration of total organic carbon in the water (Meybeck 1981). However, the proportion of carbon in the DOC pool is large relative to most rivers studied. In the average river the DOC makes up 60–80% of the total organic carbon whereas in the Kuparuk the percentage is greater than 90% (Fig. 4B). In terms of total organic carbon export from the watershed as a whole, the Kuparuk is about average with respect to rivers in temperate and boreal regions (Fig. 4C).

The output of DOC from watersheds has been found to be related to link magnitude where the number of links in a drainage is the total number of stream tributary connections (Moeller et al. 1979). The Kuparuk is a 101-link stream at the study site. The equation of Moeller et al. (1979) predicts an export of 691 $t \cdot yr^{-1}$ for the Kuparuk, while the measured values were somewhat lower (257 and 381 $t \cdot yr^{-1}$ in 1979 and 1980). While the Kuparuk has an average to high DOC concentration, the low amount of annual precipitation and runoff combines with these DOC levels to give a moderate DOC export.

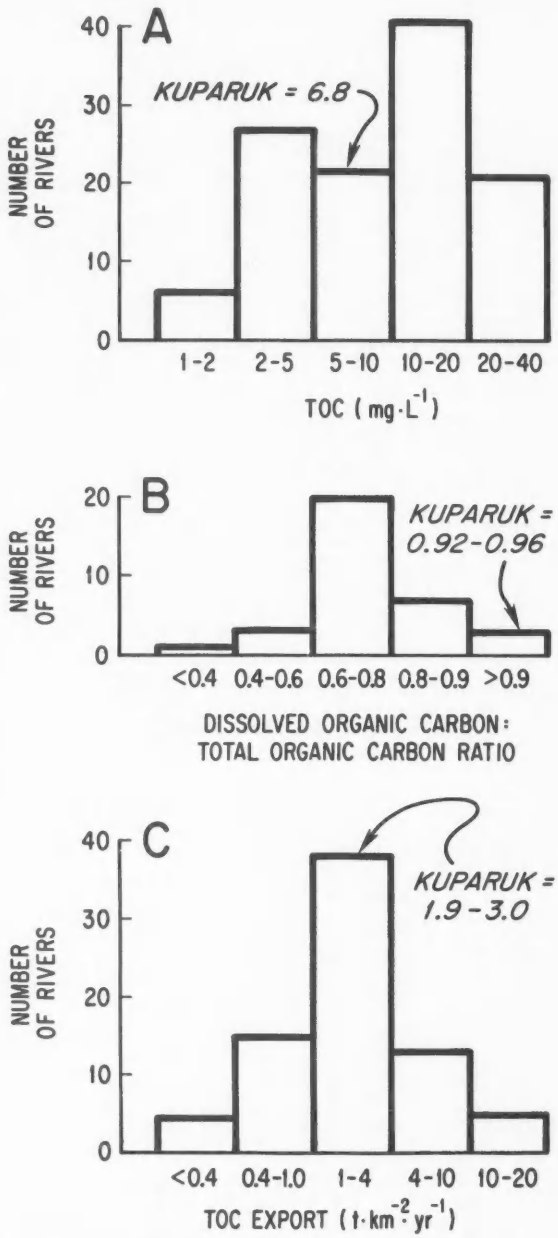

FIG. 4. Comparison of the Kuparuk River with a large spectrum of other rivers for (A) total organic carbon (TOC) concentration in the water, (B) the ratio of DOC to TOC, and (C) the export of TOC per square kilometre (adapted from Meybeck 1981).

The amount of carbon leaving the watershed as DOC and POC via the river is a small fraction of the total production of the terrestrial ecosystems; it is about 2–3% assuming 100 g $C \cdot m^{-2} \cdot yr^{-1}$ net production or 4–6% if net production is only 50 g $C \cdot m^{-2} \cdot yr^{-1}$. This is, however, substantially greater than

the DOC export to NPP ratios of 0.09–0.4% found in temperate rivers (Moeller et al. 1979). It appears that the Kuparuk is exporting a much larger fraction of the net primary production from its drainage than is commonly found in temperate streams. This may be a consquence of slow decay rates of soil carbon due to the wet soil conditions and low temperatures which result in the accumulation of peat. It may also be related to the permafrost which locks up organic matter in frozen ground for centuries and thereby stops decomposition.

In summary, the Kuparuk River is similar to many temperate streams in that allochthonous carbon inputs dominate the carbon cycle in the river in spite of the absence of shading vegetation. Much of this carbon is, however, quite refractory, much more refractory than the leaf and litter input to temperate streams. The standing stocks of chlorophyll on the rocks and the levels of gross and net primary productivity are low in comparison with temperate streams; apparently this occurs because of phosphorus limitation and the short growing season. The export of organic carbon from the watershed is about average for rivers, but since the Kuparuk watershed has low terrestrial net primary productivity, the percentage of the total watershed organic carbon production exported via the river is relatively high (2–6%). DOC is over 90% of the total export. The Kuparuk thus has a combination of characteristics which make it similar in some respects but quite different in others from boreal and temperate streams.

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References

APHA. 1975. Standard methods for the examination of water and wastewater. H. P. Orland [ed.] American Public Health Association, Washington, DC. 769 p.

BOTT, T. L., J. T. BROCK, C. E. CUSHING, S. V. GREGORY, D. KING, AND R. C. PETERSON. 1978. A comparison of methods for measuring primary productivity and community respiration in streams. Hydrobiologia 60: 3–12.

CRAIG, P. C., AND P. J. MCCART. 1975. Classification of stream types in Beauford Sea drainages between Prudhoe Bay, Alaska, and the Mackenzie Delta, N.W.T., Canada. Arct. Alp. Res. 7: 183–198.

CUMMINS, K. W., J. R. SEDELL, F. J. SWANSON, G. W. MINSHALL, S. G. FISHER, C. E. CUSHING, R. C. PETERSEN, AND R. L. VANNOTE. 1983. Organic matter budgets for stream ecosystems: problems in their evaluation, p. 299–354. *In* J. R. Barnes and G. W. Minshall [ed.] Stream ecology: application and testing of general ecological theory. Plenum Press, New York, NY. 399 p.

DUFFER, W. R., AND T. C. DORRIS. 1966. Primary production in a southern great plains stream. Limnol. Oceanogr. 11: 143–151.

DUNNE, T., AND L. B. LEOPOLD. 1978. Water in environmental planning. W. H. Freeman and Co., San Francisco, CA.

EDWARDS, R. W., AND M. OWENS. 1962. The effects of plants on river conditions. IV. The oxygen balance of a chalk stream. J. Ecol. 50: 207–220.

FISHER, S. G. 1977. Organic matter processing by a stream-segment ecosystem: Fort River, Massachusetts, U.S.A. Int. Rev. Gesamten Hydrobiol. 62: 701–727.

FISHER, S. G., AND S. R. CARPENTER. 1976. Ecosystem and macrophyte production of the Fort River, Massachusetts. Hydrobiologia 47: 175–187.

FISHER, S. G., AND G. E. LIKENS. 1973. Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. Ecol. Monogr. 43: 421–439.

HALL, C. A. S. 1972. Migration and metabolism in a temperate stream ecosystem. Ecology 53: 585–604.

HOBBIE, J. E., T. L. CORLISS, AND B. J. PETERSON. 1983. Seasonal patterns of bacterial abundance in an arctic lake. Arct. Alp. Res. 15: 253–259.

HOSKIN, C. M. 1959. Studies of oxygen metabolism of streams of North Carolina. Publ. Inst. Mar. Sci. Univ. Tex. 6: 186–192.

LANE, C. B. 1965. Metabolism of periphyton communities in two small streams. M.S. thesis, Oregon State University, Corvallis, OR. 59 p.

LEOPOLD, L. B., W. G. WOLMAN, AND J. P. MILLER. 1964. Fluvial processes in geomorphology. W. H. Freeman and Co., San Francisco, CA.

MANN, K. H., R. H. BRITTON, A. KOWALCZEWSKI, T. J. LACK, C. P. MATHEWS, AND I. MCDONALD. 1970. Productivity and energy flow at all trophic levels in the River Thames, England, p. 579–596. *In* Z. Kajak and A. Hilbricht-Ilkowska [ed.] Productivity problems of freshwaters. IBP/UNESCO Symp. Kazimierz, Dolny, Poland.

MCCONNAUGHEY, T., AND C. P. MCROY. 1979. Food-web structure and the fractionation of carbon isotopes in the Bering Sea. Mar. Biol. 53: 257–262.

MCCONNELL, W. J., AND W. F. SIGLER. 1959. Chlorophyll and productivity in a mountain stream. Limnol. Oceanogr. 4: 335–351.

MCDIFFERT, W. F., A. E. CARR, AND D. L. YOUNG. 1972. An estimate of primary production in a Pennsylvania trout stream using a diurnal oxygen curve technique. Am. Midl. Nat. 87: 564–570.

MENZEL, D., AND R. VACCARO. 1964. The measurement of dissolved and particulate carbon in seawater. Limnol. Oceanogr. 9: 138–142.

MEYBECK, M. 1981. River transport of organic carbon to the ocean, p. 219–269. *In* G. E. Likens [ed.] Flux of organic carbon by rivers to the ocean. DOE CONF.–8009140. Available from NTIS, Springfield, VA.

MINSHALL, G. W. 1978. Autotrophy in stream ecosystems. BioScience 28: 767–771.

MOELLER, J. R., G. W. MINSHALL, K. W. CUMMINS, R. C. PETERSON, C. E. CUSHING, J. R. SEDELL, AND R. L. VANNOTE. 1979. Transport of dissolved organic carbon in streams of differing physiographic characteristics. Org. Geochem. 1: 139–150.

NAIMAN, R. J. 1976. Primary production, standing stock, and export of organic matter in a Mohave Desert thermal; stream. Limnol. Oceanogr. 21: 60–73.

1983. The annual pattern and spatial distribution of aquatic oxygen metabolism in boreal forest watersheds. Ecol. Monogr. 53: 73–94.

NAIMAN, R. J., AND S. D. GERKING. 1975. Interrelationships of light, chlorophyll, and primary production in a thermal stream. Verh. Int. Ver. Limnol. 19: 1659–1664.

NAIMAN, R. J., AND J. R. SEDELL. 1980. Relationships between metabolic parameters and stream order in Oregon. Can. J. Fish. Aquat. Sci. 37: 834–847.

ODUM, H. T. 1957a. Trophic structure and productivity of Silver Springs, Florida. Ecol. Monogr. 27: 55–112.

1957b. Primary production measurements in eleven Florida springs and a marine turtle-grass community. Limnol. Oceanogr. 2: 85–97.

PETERSON, B. J., J. E. HOBBIE, AND T. L. CORLISS. 1983. A continuous-flow periphyton bioassay: tests of nutrient limitation in a tundra stream. Limnol. Oceanogr. 28: 583–591.

PETERSON, B. J., J. E. HOBBIE, A. HERSHEY, M. LOCK, T. FORD, R. VESTAL, M. HULLAR, R. VENTULLO, AND G. VOLK. 1985. Transformation of a tundra stream from heterotrophy to autotrophy by addition of phosphorus. Science (Wash., DC) 229: 1383–1386.

PROPHET, C. W., AND J. D. RANSOM. 1974. Summer stream metabolism values for Cedar Creek, Kansas. Southwest. Nat. 19: 305–308.

RAU, G. H., A. J. MEARNS, D. R. YOUNG, R. J. OLSON, H. A. SCHAFER, AND I. R. KAPLAN. 1983. Animal $^{13}C/^{12}C$ correlates with trophic level in pelagic food webs. Ecology 64: 1314–1318.

SCHELL, D. M. 1983. Carbon-13 and carbon-14 abundances in Alaskan aquatic organisms: delayed production from peat in Arctic food webs. Science (Wash., DC) 219: 1069–1071.

SEYFER, J. R., AND J. WILHM. 1977. Variation with stream order in specific composition, diversity, biomass and chlorophyll of periphyton in Otter Creek, Oklahoma. Southwest. Nat. 22: 455–467.

STOCKNER, J. G., AND K. R. S. SHORTREED. 1976. Autotrophic production in Carnation Creek, a coastal rainforest stream on Vancouver Island, British Columbia. J. Fish. Res. Board Can. 25: 1553–1563.

STRICKLAND, J. D. H. 1960. Measuring the production of marine phytoplankton. Bull. Fish. Res. Board Can. 122: 172 p.

STRICKLAND, J. D., AND T. R. PARSONS. 1965. A manual of sea water analysis. 2nd ed. Bull. Fish. Res. Board Can. 125: 203 p.

TEAL, J. M. 1957. Community metabolism in a temperate cold spring. Ecol. Monogr. 27: 282–302.

THOMAS, N., AND R. C. O'CONNELL. 1966. A method for measuring primary

production by stream benthos. Limnol. Oceanogr. 11: 386–392.

TILLY, L. J. 1968. The structure and dynamics of Cone Spring. Ecol. Monogr. 38: 169–197.

TOMINAGA, H., AND S. ICHIMURA. 1966. Ecological studies on the organic matter production in a mountain river ecosystem. Bot. Mag. (Tokyo) 79: 815–829.

UNITED STATES GEOLOGICAL SURVEY. 1980. Water resources data for Alaska. Rep. AK-80-1. NTIS, Springfield, VA. 365 p.

VANNOTE, R. G., G. W. MINSHALL, K. W. CUMMINS, J. R. SEDELL, AND C. E. CUSHING. 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. 37: 130–137.

WARREN, C. E., J. H. WALES, G. E. DAVIS, AND P. DOUDOROFF. 1964. Trout production in an experimental stream enriched with sucrose. J. Wildl. Manage. 28: 617–660.

WRIGHT, J. C., AND I. K. MILLS. 1967. Productivity studies on the Madison River, Yellowstone National Park. Limnol. Oceanogr. 12: 568–577.

Benthic Bacterial Biomass and Production in Two Blackwater Rivers

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Findlay, S., J. L. Meyer, and R. Risley. 1986. Benthic bacterial biomass and production in two blackwater rivers. Can. J. Fish. Aquat. Sci. 43: 1271–1276.

Bacterial biomass and production in sediments of two blackwater rivers were measured via epifluorescent direct counts and rate of thymidine incorporation into DNA. Biomass ranged from 3 to 1500 mg $C \cdot m^{-2}$ and production ranged from 0.01 to 22.0 mg $C \cdot m^{-2} \cdot h^{-1}$. Both biomass and production were correlated with organic content of the sediment. Neither biomass nor production was related to temperature. Allochthonous detritus apparently serves as a growth substrate for sediment bacteria. Despite differences in water chemistry and flow between the two rivers, comparison of similar sites between rivers showed similar bacterial standing stock and production. During most of the year these fourth- and sixth-order rivers are highly heterotrophic, yet at low water autochthonous carbon may serve as growth substrate for bacteria.

On a mesuré la biomasse et la production bactérienne dans les sédiments de deux rivières d'eaux noires par titrage à l'épifluorescence et taux d'incorporation de la thymidine dans l'ADN. La biomasse variait de 3 à 1 500 mg $\cdot m^{-2}$ de C et la production, de 0,01 à 22,0 mg $\cdot m^{-2} \cdot h^{-1}$ de C. La biomasse et la production dépendaient de la teneur en matière organique des sédiments. Ni la biomasse ni la production n'étaient reliées à la température. Les détritus allochtones servent apparemment de substrat de croissance des bactéries sédimentaires. Malgré les différences de chimie et de débit des eaux qui existent entre les deux rivières, la comparaison d'emplacements similaires entre elles a démontré qu'elles ont une biomasse et une production bactérienne analogue. Durant la plus grande partie de l'année, ces rivières de quatrième et sixième ordres sont fortement hétérotrophes. Cependant, à une faible concentration de carbone autochtone, elles peuvent servir de substrat de croissance des bactéries.

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There has been increasing interest in identifying the sources of organic carbon in lotic ecosystems (e.g. Benke and Wallace 1980; Conners and Naiman 1984). The influence of downstream changes in organic carbon supply on ecosystem function has been synthesized into a predictive model (Vannote et al. 1980). While the bulk of our information is derived from headwater streams, studies of larger river systems provide a test of the applicability of current concepts of lotic ecosystem structure and function. In particular, recent studies of blackwater rivers in both Canada and the United States have provided support for the River Continuum Concept (Vannote et al. 1980) as well as some modifications (Naiman 1983; Conners and Naiman 1984; Wallace and Benke 1984). High invertebrate production has been reported for a southeastern United States blackwater river (Benke et al. 1984; see also Smock et al. 1985), and this high secondary production represents an important food resource for the fishes of this river (Henry 1979). We began studies to identify sources of organic carbon in two blackwater rivers in southeast Georgia. In this paper, we examine standing stocks and production of benthic bacteria in these river systems.

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While it has long been recognized that bacteria play a key role in nutrient cycling and catabolic activity in aquatic ecosystems (Fenchel 1972; Cummins and Klug 1979), there is little information on heterotrophic bacterial production, which represents conversion of nonliving organic carbon into biomass. Clearly, catabolism and nutrient transfers accompany production of new biomass, but these processes are not necessarily directly coupled to growth and the relationship may be variable (Hanson 1980). Bacterial production represents a fundamentally different process from other aspects of "microbial activity" which have been examined. In light of the possibility that bacterial production could be a major organic carbon flux in these rivers, knowledge of factors affecting rates of production would better enable us to understand carbon flow at the system level as well as how changes in bacterial production influence other components of the ecosystem.

Study Sites

The two blackwater rivers we have studied, the Ogeechee and Black Creek, are located in the coastal plain of Georgia. At our study site, the Ogeechee River is a sixth-order river with a mean discharge of 67.7 $m^3 \cdot s^{-1}$ (U.S. Geological Survey 1982). The pH ranges from 5.5 to 7.5 and total dissolved organic carbon (DOC) concentration ranges from 4 to 34 mg

$C \cdot L^{-1}$, with highest values at high water (Meyer 1986). Black Creek, a fourth-order tributary of the Ogeechee River, has a mean discharge of 5.6 $m^3 \cdot s^{-1}$ (U.S. Geological Survey 1982). DOC concentrations are higher than in the Ogeechee, ranging from 5 to 74 mg $C \cdot L^{-1}$, again with highest values occurring during floods (Meyer 1986). The pH ranges from 4.5 to 6.5.

The predominant sediment type is a medium to coarse low-organic sand. The presence of ripples suggests a fairly high-energy hydrodynamic regime and considerable mixing of at least the top few centimetres. Therefore, the top layer of sediment is probably aerobic because the water column is well-mixed and O_2 concentrations remain high (Edwards 1985). For a more detailed site description, see Wallace and Benke (1984).

Our study sites on the Ogeechee are in Effingham Co., Georgia, just upstream of the Interstate 16 bridge. The Black Creek sites are roughly 2 km upstream from its confluence with the Ogeechee. We have sampling sites in the sandy main channels and an adjacent backwater of each river. Snags in these rivers are an important habitat for invertebrates and there can be up to 0.4 m^2 of snag surface area per square metre of river bottom (Wallace and Benke 1984).

Materials and Methods

Our sampling period spanned November 1981 – August 1983. Initially, samples were bimonthly and then once every 4–6 wk beginning in July 1982.

Sediment was collected with a PVC corer (7.5 cm diameter) which could be mounted on a length of pipe for use during flood conditions. For each site, three to four cores were taken from an area roughly 2 m in diameter. The upper 1 cm of sediment from each core was extruded into a container. This sediment layer from all cores was combined to get sufficient sediment for analysis. Our long-term sampling has dealt only with the top 1 cm. The sediment was kept at in situ temperature until return to the field laboratory (always less than 1 h). Subsamples were removed with a small plastic spoon for bacterial biomass (epifluorescent direct counts) and production (thymidine incorporation) measurements. The remaining sediment was frozen for dry weight and organic content determination. The dry weight of 2 cm^3 of sediment was measured after drying at 60°C for 48 h. Sediment organic content was determined as loss on ignition at 450°C for 12 h.

Numbers of bacterial cells were determined for three subsamples, each consisting of 2 cm^3 of sediment preserved in 5 mL of 5% buffered formalin stored at 5°C for less than 2 wk. Preserved sediment was diluted with distilled water and homogenized for 3 min in a Sorvall Omni mixer; subsamples of the homogenate were stained with acridine orange and collected on a 0.2-μm polycarbonate filter (Hobbie et al. 1977; Montagna 1982). Sonification of this sediment did not release a significantly greater number of cells than homogenization (cf. Ellery and Schleyer 1984). Numbers of bacterial cells on snags were determined by scraping the outer 1 mm of snags of known surface area into vials with 5% formalin, homogenizing, and staining as above. One filter was prepared from each subsample. On one occasion (February 1984), we measured bacterial volumes from photographs of the epifluorescent slides. The average cell volume for a given site was the weighted average of the volume of rod-shaped cells and cocci. Rods were larger than cocci (0.14 vs. 0.07 μm^3) but there was no significant difference in average cell volume between any of the sites (ANOVA, $P = 0.12$). The average cell volume (all sites combined) was 0.11 μm^3 which corresponds to 0.99 (±0.24, 1 SD) $\times 10^{-14}$ g $C \cdot cell^{-1}$ using a conversion factor of 0.09 g $C \cdot cm^{-3}$ (Cammen 1982). We have used a conversion factor of 1.0×10^{-14} g $C \cdot cell^{-1}$ to convert numbers to biomass. This value is well within the range reported for estuarine sediment bacteria (Rublee et al. 1983). Seasonal variation in average cell volume reported by Rublee (1982) for bacteria in salt marsh sediments was about 25% of the annual average.

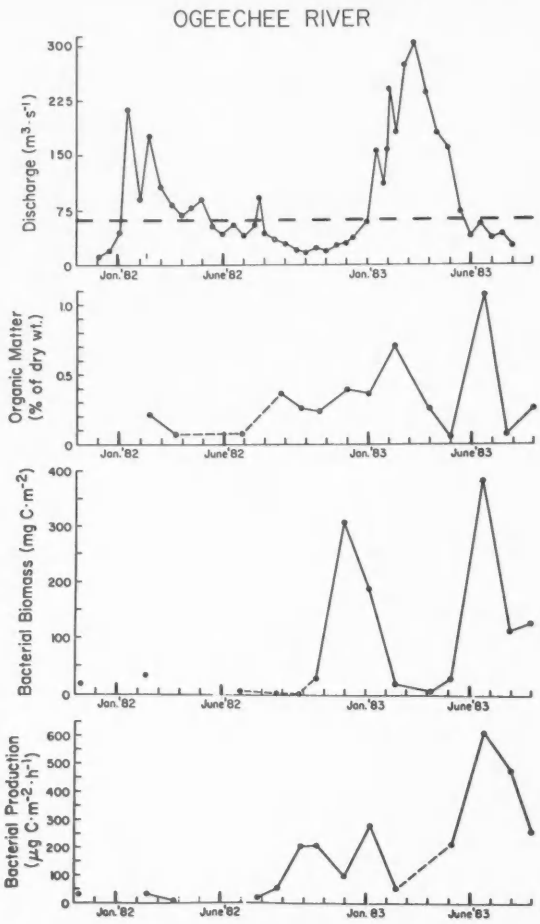

FIG. 1. Seasonal pattern of Ogeechee River discharge (weekly averages), sediment organic matter, bacterial biomass, and production for the main channel site. Sampling dates more than 6 wk apart are joined by a broken line.

Bacterial production was determined from the rate of tritiated thymidine (^{3}H-TdR) incorporation into DNA (Fuhrman and Azam 1980, 1982; Moriarty and Pollard 1981, 1982; Findlay et al. 1984). DNA synthesis is tightly coupled to cell division, so the rate of ^{3}H-TdR incorporation into DNA may be converted to production. This method relies on a number of assumptions which we have examined for this particular system (Findlay et al. 1984).

Sediment was incubated with ^{3}H-TdR (370 kBq · 2 cm^{-3} sediment, 740 kBq · $mmol^{-1}$, New England Nuclear, NET-027E) for 1 h at in situ temperature. Unincorporated label was

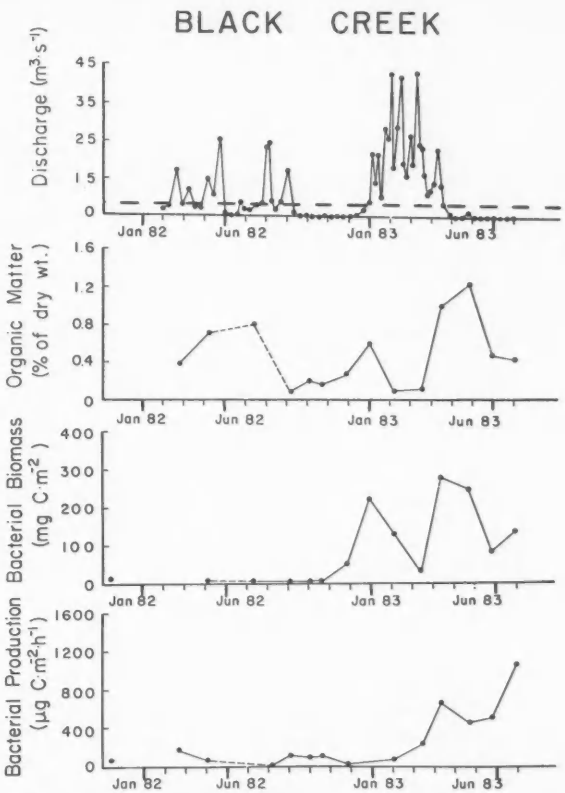

FIG. 2. Seasonal pattern of Black Creek discharge (3-d averages), sediment organic matter, bacterial biomass, and production for the main channel site. Sampling dates more than 6 wk apart are joined by a broken line.

removed by centrifugation with 5% formalin and the samples were frozen on dry ice. In the laboratory, DNA was extracted with 0.3 *M* NaOH + 25 m*M* EDTA + 0.1% SDS at 25°C for 12 h. DNA was precipitated from the chilled, acidified supernatant by high-speed centrifugation (25 000 × *g* for 15 min). The pellet was washed once with cold 5% TCA and DNA was hydrolyzed at 100°C for 30 min. Radioactivity was measured on subsamples of the final hydrolysate. The extent of dilution of ^{3}H-TdR by unlabelled TdR was determined with an isotope dilution series (Moriarty and Pollard 1981, 1982; Findlay et al. 1984). Knowing the radioactivity incorporated into DNA, the effective specific activity of the TdR pool, and a conversion factor from DNA synthesized to carbon synthesized, production may be calculated from

$$\text{Production} = (\text{DPM in DNA})/\text{SA} \times \text{cells/TdR} \times \text{C/cell} \times 10^4 \text{ cm}^3 \cdot \text{m}^{-2}$$

where production is in units of milligrams C per square metre per hour, DPM in DNA = DPM incorporated into DNA per cubic centimetre per hour, SA (specific activity) = DPM of ^{3}H-TdR added/effective pool size, cells/TdR = cells produced per mole of TdR incorporated, and C/cell = carbon content of cells (1×10^{-14} g C·cell^{-1}). Moriarty (1986), after reviewing the available information, suggested a value of 2×10^{18} cells produced·mol TdR incorporated^{-1}. The factor 10^4 cm$^3 \cdot$m^{-2} converts from cubic centimetres to the top 1 cm of an area 1 m^2. A detailed discussion of further assumptions and methodology can be found in Findlay et al. (1984).

TABLE 1. Comparison (ANOVA) of bacterial biomass (mg C·m^{-2}) and production (mg C·m^{-2}·h^{-1}) for different sites within a river and similar sites between rivers. Values are means over all sampling dates. Data followed by the same letter were not significantly different ($P > 0.05$, Student–Newman–Keuls test).

	Ogeechee		Black Creek	
	Sand	Backwater	Sand	Backwater
Biomass	92.0a	410.2b	88.2a	515.9b
Production	0.18c	3.1c	0.26c	5.9d

To determine bacterial production on snags, individual snags of known surface area were incubated, washed, and extracted just as for sediment samples.

Results

Over the course of this study, bacterial biomass ranged from 3 to 400 mg C·m^{-2} in the top 1 cm of sand sediments of both rivers. Biomass in sands of both rivers showed seasonal cycles with high values in early spring and late fall (Fig. 1, 2). The annual average biomass was 92 mg C·m^{-2}. Biomass in the high organic backwater areas of both rivers was much higher than in the sands, ranging from 40 to 1500 mg C·m^{-2} with an annual average of about 450 mg C·m^{-2}. There were also temporal changes in biomass in these backwaters but the pattern was not clear-cut.

Bacterial production in the sands of Black Creek ranged from 10 to 1100 μg C·m^{-2}·h^{-1} with peak values in spring and fall (Fig. 2). Production in the sand of the Ogeechee ranged from 10 to 620 μg C·m^{-2}·h^{-1} with the maximum in fall. Bacterial production in the backwaters of both rivers was about an order of magnitude greater than in the sandy sediments and ranged from 0.13 to 22.1 mg C·m^{-2}·h^{-1}.

Comparisons of similar sites between rivers and different sites within a river show that there was no "river effect" in that bacterial biomass and production at the two sand sites (= main channel) were similar and the two backwaters were similar (Table 1). There was a "site effect" within a river with significant differences in biomass and production between sand and backwater sites. The one exception was no difference in production between the sand and backwater site of the Ogeechee River. The site initially selected as a backwater in the Ogeechee becomes part of the main channel during floods, which probably explains the similarity.

There was no correlation ($P > 0.05$) between either biomass per square metre or production per square metre and temperature ($P > 0.05$) for any individual site or when the data from all sites were combined. Both biomass and production were significantly correlated with sediment organic content (Fig. 3) (see also Dale 1974). Similar calculations for each site separately showed positive relationships between biomass and organic content (Table 2). Plots of production versus organic content showed outlying points with a far greater production than would be predicted from the general trend (e.g. Fig. 4). Following the suggestion of Bliss (1967), linear regression was calculated without the suspected outliers. Points lying outside the 95% confidence limits for predicted values were excluded from the correlation analysis. There was one such

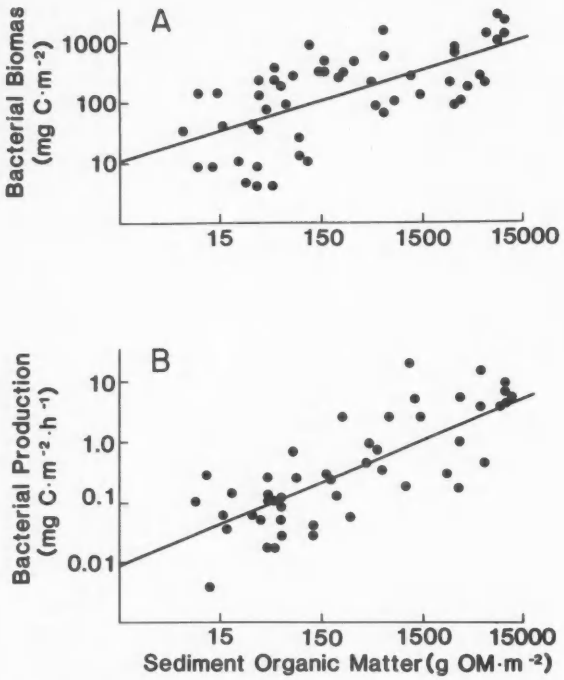

FIG. 3. (A) Relationship between bacterial biomass and sediment organic content ($\log_e$ (B) = 1.92 + 0.499 $\log_e$ (g OM·m^{-2}); $r^2 = 0.69$, $P < 0.001$, $N = 52$). (B) Relationship between bacterial production and sediment organic content ($\log_e$ (P) = −4.84 + 0.705 $\log_e$ (g OM·m^{-2}); $r^2 = 0.57$, $P < 0.001$, $N = 49$). Data from all sites and times combined.

point for each sand site and the backwater of Black Creek. We have reason to believe (see Discussion) that these high values were due to bacteria using autochthonous primary production as a growth substrate rather than sediment organic matter. Eliminating these outliers reveals significant ($P < 0.05$) positive correlations between production and sediment organic content for all sites except the backwater of the Ogeechee River (Table 2). Because this site becomes part of the main channel during floods, this change in hydrology probably accounts for the lack of pattern.

There was no clear pattern to temporal or spatial changes in bacterial biomass or production on snags (data not shown). Both biomass (0.4 mg C·m^{-2}) and production on snags (~25 μg C·m^{-2}·h^{-1}) were low relative to a square metre of sand (92 mg C·m^{-2}; 180 μg C·m^{-2}·h^{-1}).

Discussion

The range in bacterial cell numbers found for all sites combined over the course of this study (0.2×10^9 to 50×10^9 cells·g dry wt.$^{-1}$; organic matter (OM) = 0.05–56% of dry wt.) was lower than the range in cell numbers reported for marine sediments with a narrower range in organic content (2×10^9 to 100×10^9 cells·g dry wt.$^{-1}$; OM = 0.4–3%) (Cammen 1982). Also, average bacterial production in the sand sediments of the Ogeechee River was 4.3 mg C·m^{-2}·d^{-1}, which is substantially lower than production reported for marine sediments of comparable organic content (cf. Fallon

TABLE 2. Pearson correlation coefficients between bacterial biomass or production and sediment organic content for each site. Production values determined to be outliers were omitted (see text).

	Biomass with organic content			Production with organic content		
	r	P	N	r	P	N
Ogeechee River						
sand site	0.65	<0.05	12	0.60	0.05	11
backwater	0.39	0.21	12	−0.13	0.7	10
Black Creek						
sand site	0.63	<0.05	12	0.69	<0.05	11
backwater	0.73	<0.05	14	0.63	<0.05	12

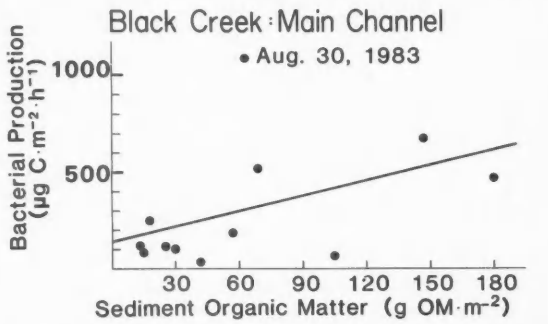

FIG. 4. Relationship between bacterial production and sediment organic matter for the main channel of Black Creek. The point labelled (Aug. 30, 1983) is from a period of high primary production.

et al. 1983 (21 mg C·m^{-2}·d^{-1}) and Moriarty and Pollard 1982 (~50 mg C·m^{-2}·d^{-1})). Whether these observations are part of a pattern of lower biomass and production in freshwater sediments awaits further study.

Over the 18-mo period, the temporal variability about the mean value of either biomass or production was quite high for all sites, with coefficients of variation ranging from 77 to 189%. We suggest that changes in organic matter were responsible for the fluctuations (Fig. 3). There is a well-known inverse relationship between sediment organic content and particle size (Cammen 1982), and it is impossible to unequivocally separate the influence of these two factors (Bott and Kaplan 1985). Experimental results support our contention that organic matter rather than particle size was the proximal cause of this relationship. Additions of particulate oak leaf detritus to Ogeechee River sediment led to a doubling of bacterial production (Findlay et al., unpubl. data), yet the magnitude of these organic matter additions (<0.4 mg OM·g dry wt.$^{-1}$) would have a small effect on the bulk properties of this sediment.

There are two possible sources of this organic carbon: autochthonous primary production or allochthonous inputs. We think this was allochthonous material because annual export from the Ogeechee floodplain (Cuffney 1984) was 75 times greater than annual average autochthonous primary production (Edwards 1985). Moreover, one of the more rapid increases in benthic organic matter (~1.3 g OM·m^{-2}·d^{-1}, January–February 1983) in the Ogeechee River occurred when system-level gross primary production was only ~0.7 g OM·m^{-2}·d^{-1} and P/R was <0.4 (Edwards 1985). This allochthonous mate-

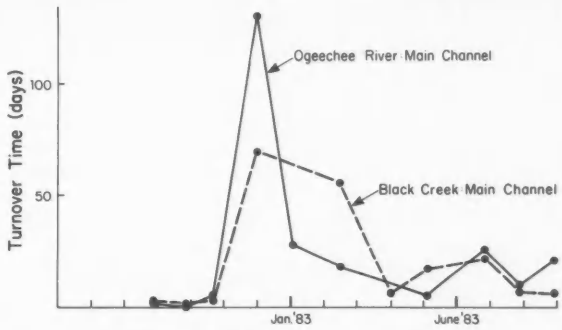

FIG. 5. Turnover time of bacterial biomass at the main channel site of the Ogeechee River and Black Creek.

rial may have originally entered the river upstream of our immediate study area, since the Ogeechee and its tributaries are bounded by floodplain for much of its length. The importance of floodplain–river exchanges has been emphasized by Mulholland (1981) for a similar system.

We have circumstantial evidence that there was also input of nongrowing bacteria to these sediments. The turnover time ($B \cdot P^{-1}$) of bacteria in both rivers rose sharply in December 1982 (Fig. 5). The increase in turnover time was due to an increase in biomass during a period of decreasing production. Production at this time was not unusually low; thus, the biomass increase was probably responsible for the longer turnover time. Turnover times of this magnitude (50–100 d, Fig. 5) are much longer than reported for other sediment bacterial assemblages (Moriarty and Pollard 1982; Fallon et al. 1983; Bott and Kaplan 1985). We calculated, from the change in biomass, what rates of production would be necessary to account for these increases in biomass. For the Ogeechee River, production over this interval would have had to be 300 μg $C \cdot m^{-2} \cdot h^{-1}$ when measured production during the previous 4 wk was actually declining from 230 to 100 μg $C \cdot m^{-2} \cdot h^{-1}$ (Fig. 1). For Black Creek, production would have had to be 200 μg $C \cdot m^{-2} \cdot h^{-1}$ over the interval when actual production over the previous 3 mo was always less than 110 μg $C \cdot m^{-2} \cdot h^{-1}$ (Fig. 2). Furthermore, these required production estimates are minimum estimates because there were almost certainly processes such as grazing removing cells over this interval. Apparently, some process other than in situ growth was responsible for this increase in bacterial biomass.

One possible source of cells was bacteria attached to allochthonous material transported from the floodplain or upstream. Leaf litter on the floodplain was well colonized by bacteria (Cuffney 1984), and these cells may retain their integrity after being carried into the river. These cells appeared to be dormant or growing very slowly; otherwise their production would have decreased the turnover times. Similarly, data on water column bacteria showed a large increase in number of cells during a period of low production when the river was on the floodplain (Edwards 1985). These data strengthen our assertion that there was transport of nongrowing cells into the Ogeechee River. This observation is not unprecedented; Ducklow et al. (1982) found that the vertical flux of bacteria into sediment traps deployed in the Hudson River plume was 10 times greater than in situ production.

There were obvious outliers on the graphs of production versus sediment organic content (Fig. 4). These points were from the summer (July–August 1983) at low flow conditions, coinciding with one of the few periods when significant benthic primary production could occur. During most of the year, light extinction was so great that benthic primary production was only 0.2–0.4 mg $C \cdot m^{-2} \cdot h^{-1}$, but during late summer 1983, benthic primary production increased to 4–6 mg $C \cdot m^{-2} \cdot h^{-1}$ (L. Dunn, Department of Biology, Georgia Institute of Technology, Atlanta, GA 30332, unpubl. data). Heterotrophic bacterial production at this time was 0.3 mg $C \cdot m^{-2} \cdot h^{-1}$, and assuming that bacteria convert half of carbon assimilated into new biomass (c.f. Moriarty and Pollard 1982), only 0.6 mg $C \cdot m^{-2} \cdot h^{-1}$ would be required to support this bacterial production. Thus, it is quite feasible that algal production is subsidizing bacterial production by providing "high-quality" organic carbon. Such a pattern has been suggested based on the relationship between bacteria and primary production in the plankton (Cole et al. 1982; Azam et al. 1983) and in an experimentally enriched stream (Peterson et al. 1985).

Our results generally support the emerging picture of higher-order blackwater rivers as strongly heterotrophic systems which appear to rely on inputs of organic matter from their extensive floodplains. For most of the year, allochthonous carbon is the most important bacterial growth substrate. Despite the strong bias towards heterotrophy, at low water when light can reach the benthos, the system becomes more autotrophic and in situ primary production may become an important source of reduced carbon for bacteria. It is the organic matter supply, not temperature, that is the best predictor of benthic bacterial biomass and production. Therefore, the nature of this system changes depending upon hydrology. In contrast with other higher-order rivers, interactions between the river and riparian zone are at least as important as for lower-order streams.

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References

AZAM, F., T. FENCHEL, J. FIELD, J. GRAY, L. A. MEYER-REIL, AND F. THINGSTAD. 1983. The ecological role of water-column microbes in the sea. Mar. Ecol. Prog. Ser. 10: 257–263.

BENKE, A. C., T. ARSDALL, AND D. GILLESPIE. 1984. Invertebrate productivity in a subtropical blackwater river: the importance of habitat and life history. Ecol. Monogr. 54: 25–63.

BENKE, A. C., AND J. B. WALLACE. 1980. Trophic basis of production among net-spinning caddisflies in a southern appalachian stream. Ecology 61: 108–118.

BLISS, C. I. 1967. Statistics in biology. Vol. 1. McGraw-Hill, New York, NY. 558 p.

BOTT, T. L., AND L. A. KAPLAN. 1985. Bacterial biomass, metabolic state, and activity in stream sediments: relation to environmental variables and multiple assay comparisons. Appl. Environ. Microbiol. 50: 508–522.

CAMMEN, L. 1982. Effect of particle size on organic content and microbial abundance within four marine sediments. Mar. Ecol. Prog. Ser. 9: 273–280.

COLE, J., G. LIKENS, AND D. STRAYER. 1982. Photosynthetically produced dissolved organic carbon: an important carbon source for planktonic bacteria. Limnol. Oceanogr. 27: 1080–1090.

CONNERS, M. E., AND R. J. NAIMAN. 1984. Particulate allochthonous inputs; relationships with stream size in an undisturbed watershed. Can. J. Fish. Aquat. Sci. 41: 1473–1484.

CUFFNEY, T. F. 1984. Characteristics of riparian flooding and its impact upon the processing and exchange of organic matter in coastal plains streams of Georgia. Ph.D. dissertation, University of Georgia, Athens, GA. 168 p.

CUMMINS, K., AND M. KLUG. 1979. Feeding ecology of stream invertebrates. Annu. Rev. Ecol. Syst. 10: 147–172.

DALE, N.G. 1974. Bacteria in intertidal sediments: factors related to their distribution. Limnol. Oceanogr. 19: 509–518.

DUCKLOW, H., D. KIRCHMAN, AND G. ROWE. 1982. Production and vertical flux of attached bacteria in the Hudson River plume of the New York bight as studied with floating sediment traps. Appl. Environ. Microbiol. 43: 769–776.

EDWARDS, R. 1985. The role of seston bacteria in the metabolism and secondary production dynamics of southeastern blackwater rivers. Ph.D. dissertation, University of Georgia, Athens, GA. 174 p.

ELLERY, W. N., AND M. SCHLEYER. 1984. Comparison of homogenization and ultrasonication as techniques in extracting attached sedimentary bacteria. Mar. Ecol. Prog. Ser. 15: 247–250.

FALLON, R., S. NEWELL, AND C. HOPKINSON. 1983. Bacterial production in marine sediments: will cell-specific measures agree with whole system metabolism? Mar. Ecol. Prog. Ser. 11: 119–127.

FENCHEL, T. 1972. Aspects of decomposer food chains in marine benthos. Verh. Dtsch. Zool. Ges. 65: 14–22.

FINDLAY, S., J. MEYER, AND R. EDWARDS. 1984. Measuring bacterial production via rate of incorporation of [^{3}H] thymidine into DNA. J. Microbiol. Meth. 2: 57–72.

FUHRMAN, J. A., AND F. AZAM. 1980. Bacterioplankton secondary production estimates for coastal waters of British Columbia, Antarctica and California. Appl. Environ. Microbiol. 39: 1085–1095.

1982. Thymidine incorporation as a measure of heterotrophic bacterioplankton production in marine surface waters: evaluation and field results. Mar. Biol. 66: 109–120.

HANSON, R. 1980. Measuring microbial activity to assess detrital decay and utilization, p. 347–357. *In* K. Tenore and B. Coull [ed.] Marine benthic dynamics. University of South Carolina Press, Columbia, SC.

HENRY, R. L. 1979. Food habits and feeding relationships of Satilla River fishes. M.S. thesis, Georgia Institute of Technology, Atlanta, GA. 89 p.

HOBBIE, J. E., R. J. DALEY, AND S. JASPER. 1977. Use of nucleopore filters for counting bacteria by fluorescent microscopy. Appl. Environ. Microbiol. 33: 1225–1228.

MEYER, J. 1986. Dissolved organic carbon dynamics in two subtropical blackwater rivers. Arch. Hydrobiol. (In press)

MONTAGNA, P. A. 1982. Sampling design and enumeration statistics for bacteria extracted from marine sediments. Appl. Environ. Microbiol. 43: 1366–1372.

MORIARTY, D. 1986. Measurement of bacterial growth rates in aquatic systems using rates of nucleic acid synthesis. Adv. Aquat. Microbiol. (In press)

MORIARTY, D., AND P. POLLARD. 1981. DNA synthesis as a measure of bacterial productivity in seagrass sediments. Mar. Ecol. Prog. Ser. 5: 151–156.

1982. Diel variation of bacterial productivity in seagrass (*Zostera capricornii*) beds measured by rate of thymidine incorporation into DNA. Mar. Biol. 72: 165–173.

MULHOLLAND, P. J. 1981. Organic carbon flow in a swamp-stream ecosystem. Ecol. Monogr. 51: 307–322.

NAIMAN, R. J. 1983. The annual pattern and spatial distribution of aquatic oxygen metabolism in boreal forest watersheds. Ecol. Monogr. 53: 73–94.

PETERSON, B., J. HOBBIE, A. HERSHEY, M. LOCK, T. FORD, J. VESTAL, V. MCKINLEY, M. HULLER, M. MILLER, R. VENTULLO, AND G. VOLK. 1985. Transformation of a tundra river from heterotrophy to autotrophy by addition of phosphorus. Science (Wash., DC) 229: 1383–1386.

RUBLEE, P. 1982. Seasonal distribution of bacteria in salt marsh sediments in North Carolina. Estuarine Coastal Shelf Sci. 15: 67–74.

RUBLEE, P., S. M. MERKEL, AND M. FAUST. 1983. The transport of bacteria in the sediments of a temperate marsh. Estuarine Coastal Shelf Sci. 16: 501–509.

SMOCK, L., E. GILINSKY, AND D. STONEBURNER. 1985. Macroinvertebrate production in a southeastern United States blackwater stream. Ecology 66: 1491–1503.

UNITED STATES GEOLOGICAL SURVEY. 1982. Water resources data for Georgia. Water-data Report GA-82-1.

VANNOTE, R., G. MINSHALL, K. CUMMINS, J. SEDELL, AND C. CUSHING. 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. 37: 130–137.

WALLACE, J. B., AND A. C. BENKE. 1984. Quantification of wood habitat in subtropical coastal plain streams. Can. J. Fish. Aquat. Sci. 41: 1643–1652.

Theory, Practice, and Effects of *Mysis relicta* Introductions to North American and Scandinavian Lakes

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Fisheries biologists have greatly altered the natural distribution of the crustacean *Mysis relicta* by introducing it into many lakes in both North America and Scandinavia to serve as a supplementary food source for fish. The original concept of *Mysis* as a deepwater benthic organism which remains isolated in the profundal zone of lakes needs to be modified to include its downstream dispersal capabilities. After introduction to a lake, *Mysis* will probably eventually reach all lakes in the downstream watershed. Recent studies indicate that rates of increase of introduced *Mysis* populations probably depend on available food and temperature. As well, introduced populations have been shown to modify benthic, phytoplankton, zooplankton, and fish communities. Most *Mysis* introductions have taken place without consideration of general criteria suggested for introduced species.

Les biologistes des pêches ont fortement modifié la distribution naturelle du crustacé *Mysis relicta* en l'introduisant dans de nombreux lacs, tant en Amérique du Nord qu'en Scandinavie, pour qu'il serve de supplément alimentaire aux poissons. Il faut modifier le concept original de *Mysis*, en tant qu'organisme benthique qui demeure isolé dans les profondeurs des lacs, pour tenir compte de ses capacités de dispersion en aval. Après son introduction dans un lac, *Mysis* colonisera probablement tous les lacs en aval du bassin hydrographique. Des études récentes indiquent que les taux d'accroissement des populations de *Mysis* introduites dépendent des aliments disponibles et de la température. Par ailleurs, il a été démontré que les populations introduites modifient les populations benthiques de phytoplancton, de zooplancton et de poissons. La plupart des introductions de *Mysis* ont été faites sans tenir compte des critères généraux proposés pour les espèces introduites.

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Since the crustacean *Mysis relicta* was first recognized as an important item in the diet of freshwater fish species (Wells and Beeton 1963; Dryer et al. 1965; and others), fisheries managers have been substantially altering the zoogeographical distribution of the species. They have introduced this so-called "freshwater shrimp" into lakes in both North America and Scandinavia to serve as a supplementary food source for fish. In general it was thought that the introductions would enhance fish production by providing sizable and available energy sources for fish where food was limiting. This review summarizes the theory and practice of introductions in both North America and Scandinavia and evaluates their results and effectiveness.[1]

Rationale For Introductions

The first suggestion for *Mysis* introductions in North America was made in 1939 by W. A. Clemens, an active and well-respected zoologist and fishery biologist in Canada. He recommended that if any attempt was to be made to develop a

[1]An update of material presented at the symposium on mysid ecology at the 1981 meetings of the American Society of Limnology and Oceanography held in Milwaukee, Wisconsin.

commercial fishery for lake whitefish (*Coregonus clupeaformis*) in the Okanagan lakes of British Columbia, the introduction of *Pontoporeia affinis* and *Mysis relicta* should be considered (Clemens et al. 1939; see also Larkin 1952). In eastern Canadian and American lakes where lake whitefish supported major commercial fisheries, *Pontoporeia* and *Mysis* provided a large proportion of their food. In 1949, the recommendation was acted upon by Dr. Peter Larkin, then Chief Fishery Biologist with the B.C. Game Commission in British Columbia (Larkin 1951). In Kootenay Lake the growth rate of rainbow trout (*Salmo gairdneri*) apparently slowed between the ages of 1 and 3 yr during the period when trout shifted from feeding on zooplankton to feeding on fish. Provincial fisheries biologists concluded that there was no food item of suitable size, abundance, and availability to be utilized by the trout during their transition from planktivory to piscivory. *Mysis* and *Pontoporeia* were introduced into Kootenay Lake in 1949 and 1950 (Sparrow et al. 1964) with the hope that these species would provide the appropriate food items in sufficient abundance to bridge this dietary gap. Although the growth response of the target species, rainbow trout, was disappointing, the increased growth rate and size of the kokanee (*Oncorhynchus nerka*) in the lake has been used as a rationale for further introductions in North America (Northcote 1970).

In Scandinavia, the rationale for *Mysis* introductions was different. Most inland lakes in these countries are in high mountainous terrain and are controlled for hydroelectric purposes, with fluctuations in water level from 50 to 20 m. In winter when the water level is low, the littoral zone becomes frozen, dried out, and later badly eroded, resulting in a quantitative reduction of the bottom fauna (Grimås 1961). As a result of such regulation, the brown trout (*Salmo trutta*), which inhabits the upper littoral zone, decreased in numbers and growth rate. The growth rate of char (*Salvelinus stagnalis*) also decreased (Fürst 1972a). It was hypothesized (Fürst 1972a) that in these lakes, *Mysis relicta* would be trophically independent of the littoral zone and could act as an energy "elevator" during its vertical migration, feeding on benthic organic detritus by day and transporting this energy, which would normally be "lost" to the system, to the fish population near the surface at night. Also, *Mysis* would be available as fish food during the winter when little else was available (Fürst et al. 1978). Although the potential impact of *Mysis* introductions into these lakes was not known, it was argued that the only way to determine the effect of *Mysis* on the lake community was to carry out the introductions. As well, the fish populations in these lakes were so severely affected it was felt that *Mysis* introductions could only improve the situation (Fürst et al. 1978).

Postglacial Mysis Distribution and Extension by Introductions

In North America, the natural distribution of *Mysis relicta* closely follows the maximum extent of Pleistocene glaciation (Dadswell 1974; Fig. 1). However, *Mysis* has become widely spread to the south and west of its natural range since introductions were started in 1949 (Fig. 1). Some, but by no means all, of the many introductions were recorded by Stringer (1967) and Gosho (1975). In British Columbia alone, 21 documented introductions have taken place up to and including 1980 (Table 1). In the United States, over 100 documented introductions have taken place and many undocumented introductions have been carried out. Often the origin of the introduced stock is impossible to trace because of the many secondary introductions.

In Scandinavia, the natural distribution of *Mysis* follows the highest shoreline of the former Baltic Sea (Fig. 2). All natural lakes in which *Mysis* occurs naturally are below this shoreline. In Norway there have been approximately nine introductions, in Finland at least one, and in Sweden, 61. Of the Swedish transplants, new populations are known to have been established in about 50 cases. Nine introductions are known to have been unsuccessful; the causes of the failures are suspected to be low stocking densities, low pH (5.8–5.5), or both (Fürst 1981).

In some Swedish river systems, *Mysis* has dispersed downstream and established new populations. For example, in 1957, *Mysis* was first introduced into Lake Torrön, at the head of the Indalsälven River system. By 1967 it had spread downstream several hundred kilometres (Fürst 1981). Another example is provided by the introduced *Mysis* population in Lake Blåsjön. *Mysis* was first found in Lake Blåsjön in trawl hauls in 1966, 2 yr after its introduction (Fürst 1972a). Fourteen years later, *Mysis* was found in Lake Russfjärden, 240 km downstream, having passed through four hydroelectric stations, 12 lakes, and many rapids. Similar downstream dispersal has been observed in North America. *Mysis* now occurs in Skaha Lake, having drifted downstream from Okanagan Lake where it was first introduced in 1966 (Alan Martin, Regional Fisheries Biologist, British Columbia Fisheries Branch, Cranbrook, B.C., pers. comm.).

The concept of *Mysis* as a deepwater benthic organism which remains isolated in the profundal zone needs to be modified to include its downstream dispersal capabilities. Not only is its present distribution rapidly changing because of introductions, but downstream dispersal is also altering its zoogeographical distribution. *Mysis* is not only introduced into a lake, but in time probably into all suitable lakes downstream.

Rate of Increase and Establishment

One of the problems of determining the rate of increase of a *Mysis* population once founding individuals have been introduced into a lake is that very few long-term studies have been carried out. The usual practice is to introduce the animals and wait for the effects, hopefully favorable. As is shown in Table 1, only 18 of the 21 lakes in British Columbia into which *Mysis* has been introduced have been resampled. As well, mysids are difficult to sample quantitatively although several recent studies have suggested that vertical net hauls on moonless nights provide a reliable method for obtaining estimates of *Mysis* in the water column (Nero and Davies 1982; Grossnickle and Morgan 1979).

Once introduced into a lake, the rate of population increase of *Mysis* may depend on such factors as available food and temperature. Fürst (1972a, 1972b) found that within 10 yr after *Mysis* was transplanted from Lake Vättern, where it matured in 1 yr, to the more oligotrophic Lake Torrön, its growth rate slowed and part of the population matured in 2 yr. Fürst suggested that intraspecific competition for food was responsible for the decreased growth. As the introduced population grew more dense, food became limiting, and an increased proportion of the *Mysis* matured in 2 yr. Fürst also suggested that there was an hereditary tendency to keep a 1-yr life history, since males in Lake Torrön matured in 1 yr, despite extremely slow growth

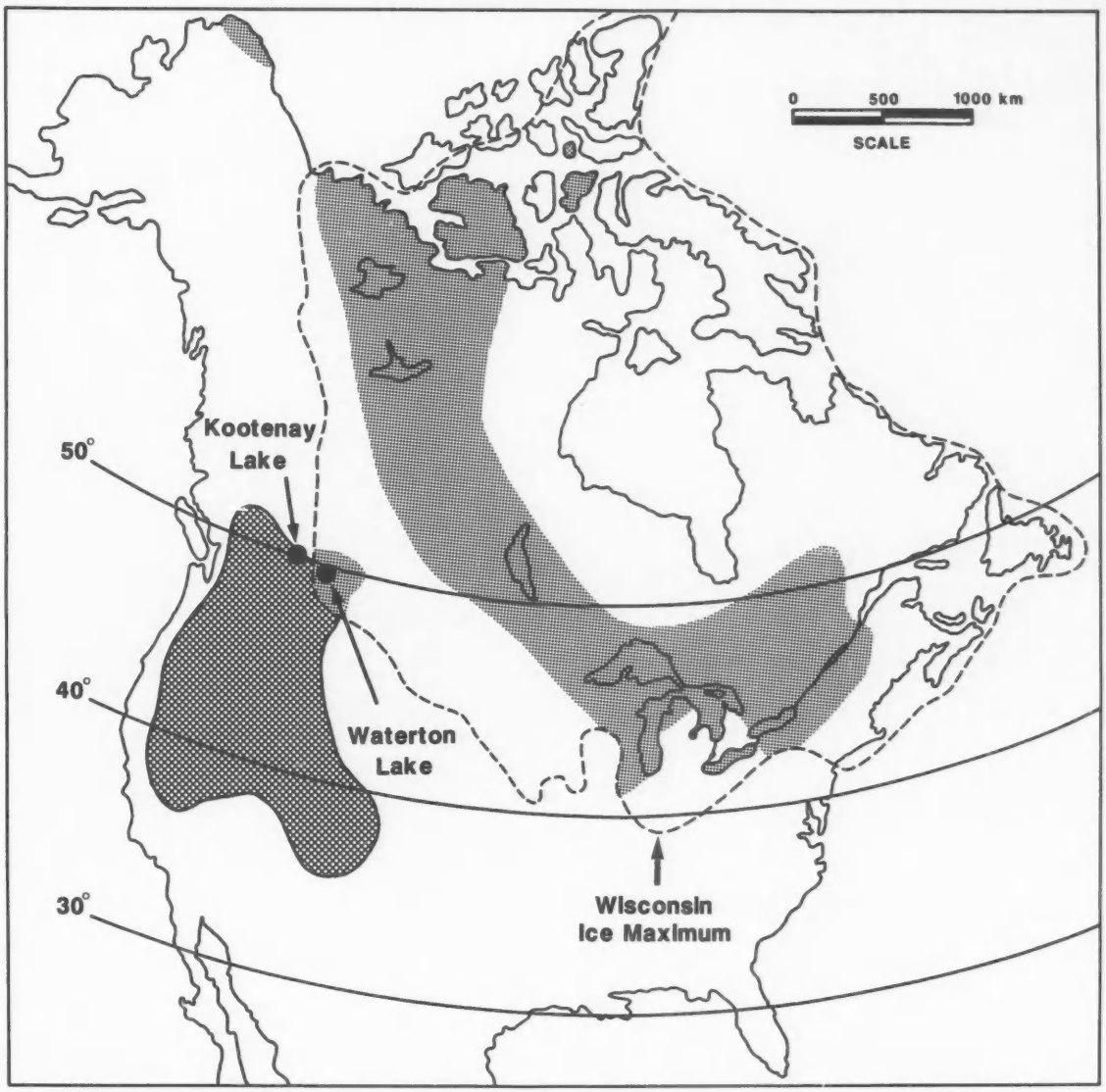

FIG. 1. Generalized natural distribution of *Mysis relicta* in North America (light shading) and its extended range (dark shading) through introductions (see Dadswell 1974 for details of natural distribution).

and small size. *Mysis* was also introduced from Lake Jansjön, where it matured in 1 yr, to Lake Blåsjön. During the first few years in Blåsjön, *Mysis* had a 1-yr life history which slowly changed to a 2-yr life history. Morgan (1981) has shown that lake trophic status can be correlated with *Mysis* life history, time to maturity being 1 yr in eutrophic lakes and 2–4 yr in meso- and oligotrophic lakes. Similarly, Berrill and Lasenby (1983) have demonstrated that time to maturity can be controlled by temperature; *Mysis* raised at temperatures greater than 8°C mature in 8 mo, whereas those raised at less than 8°C take at least 1 yr to mature. Both trophic status and hypolimnetic temperatures are related to lake morphometry (Wetzel 1983), a factor that may ultimately control life history and population increase. The following examples illustrate the kinds of differences that can occur.

In 1949 and 1950, 12 000 mysids were introduced into Kootenay Lake (Sparrow et al. 1964), a large intermontane lake in southeastern British Columbia (z_{max} = 154, A = 389 km^2). In the early 1960's they were found in fish stomachs (Dolly Varden, *Salvelinus malma*; kokanee; mountain whitefish, *Prosopium williamson*; burbot, *Lota lota*), particularly in the West Arm of the lake (Northcote 1972) but also in these species and rainbow trout in the main lake (Northcote 1973). By assembling the information on *Mysis* population density from various sources, Daley et al. (1981) have shown that the *Mysis* population in Kootenay Lake was still increasing up to

TABLE 1. Transplants of *Mysis relicta* into British Columbia lakes (modified from G. E. Stringer, B.C. Fisheries Branch, Kamloops, B.C., unpubl. data) (? = not determined; + = positive effect; − = negative effect; 0 = no effect).[a]

Lake	Year(s) introduced	No. released	Stock source	Viable population established	Target species	Apparent effect on target fish species	
						Size	Abundance
Arrow (upper)	1968	100 000	Kootenay	Yes	Kokanee	+	−
	1974	500 000	Kootenay				
Arrow (lower)	1974	100 000	Kootenay	Yes	Kokanee	+	−
Cameron	1973	150 000	Kootenay	No	Kokanee		
Canim	1967	325 000	Kootenay	Yes	Kokanee	?	−
	1968	300 000	Kootenay		Lake trout		
Christina	1968	80 000	Kootenay	Yes	Kokanee	0	?
Duncan	1975	100 000	Kootenay	?	Kokanee	0	0
Echo	1980	225 000	Pinaus	?	Kokanee		
Grave	1979	250 000	Moyle	No	Kokanee	0	0
					Rainbow		
Kalamalka	1965	145 000	Kootenay	Yes	Kokanee	0	−
	1966	95 000	Kootenay				
Kootenay	1949	12 500	Waterton	Yes	Rainbow	+	−
	1950				Kokanee	+	?
					Mt. whitefish	+	?
Lac la Hoche	1975	30 000	Canim	No	Kokanee	0	?
	1976	350 000	Canim				
Missezula	1975	20 000	Okanagan	No	Kokanee	0	?
	1976	200 000	Okanagan	No			
Moyle	1970	250 000	Kootenay	Yes	Kokanee	0	−
Okanagon	1966	240 000	Kootenay	Yes	Kokanee	+	−
Otter	1975	?	Okanagan	?	Kokanee	0	?
Pinaus	1965	80 000	Kootenay	Yes	Rainbow	+	?
	1966	90 000	Kootenay				
Skaha			Downstream drift from Okanagan	Yes	Kokanee	+	−
Slocan	1973 / 1974	200 000	Kootenay	Yes	Kokanee	+	?
Whatsam	1974	100 000	Kootenay	No	Kokanee	?	?
Wood	1966	90 000	Kootenay	No	Kokanee	+	−

[a]Transplants in some areas of North America are well documented but are undocumented and difficult to trace in other areas.

the early 1980's (Fig. 3).

Mysis was introduced into Lake Tahoe, California–Nevada, from 1963 to 1965. Approximately 333 000 mysids were transported from Waterton Lake (Fig. 1) and introduced at various locations around Lake Tahoe, a cold, deep, ultraoligotrophic lake (Linn and Frantz 1965; Hansen 1966). *Mysis* appeared in large numbers in epibenthic sled tows and lake trout (*Salvelinus namaycush*) stomachs by 1971 (Richards et al. 1975; Morgan et al. 1978). Similar patterns have been found in other lakes, but with the time of first appearance of *Mysis* in fish stomachs ranging from 4 yr in Lake Mesvattnet to as long as 16 yr in Kootenay Lake (Fig. 3).

Effect on the Benthic Community

Very little information exists on the effect of *Mysis* on benthic communities. However, lake morphometry and trophic status influence the distribution of *Mysis* populations. In many deep lakes, *Mysis* remains pelagic during its diel migration whereas in shallower lakes virtually the whole population reaches the sediment–water interface during the daytime (Morgan et al. 1978; Daley et al. 1981). In large lakes such as Kootenay, with differing regional characteristics, mysids in the day may form pelagic, midwater layers in some parts of the lake and benthic populations in others (Northcote 1972; Robertson et al. 1968). *Mysis* also avoids anaerobic bottom regions often found in eutrophic lakes (Lasenby 1971).

Mysis seems to display a variety of feeding habits while at the sediment–water interface. Inorganic and organic bottom sediments are found in mysid guts (Grossnickle 1982) as well as chironomid head capsules (Lasenby and Langford 1973). In addition, direct predation on *Pontoporeia* in the Laurentian Great Lakes (Parker 1980) and the benthic cladoceran *Eurycercus* (Lasenby and Fürst 1981) has been observed. Fürst et al. (1978) even noted the area-by-area disappearance of the benthic cladoceran *Eurycercus* in Lake Blåsjön as the introduced *Mysis* population spread throughout the lake. Further evidence for *Mysis* feeding on the sediments is provided by Evans and Lasenby (1983), who showed a positive correlation between lead concentration in sediment and *Mysis* lead concentration for Kootenay Lake, suggesting that the mysids are ingesting lead-contaminated sediments.

Effect on the Plankton Community

Phytoplankton has long been known as an important com-

FIG. 2. Highest shoreline (broken line) of the former Baltic Sea (shaded area) in Sweden and sites of *Mysis* introductions (solid circles). Open circles represent the donor lakes. Arrows indicate locations of documented downstream dispersal of *Mysis* populations after introductions (adapted from Fürst 1981).

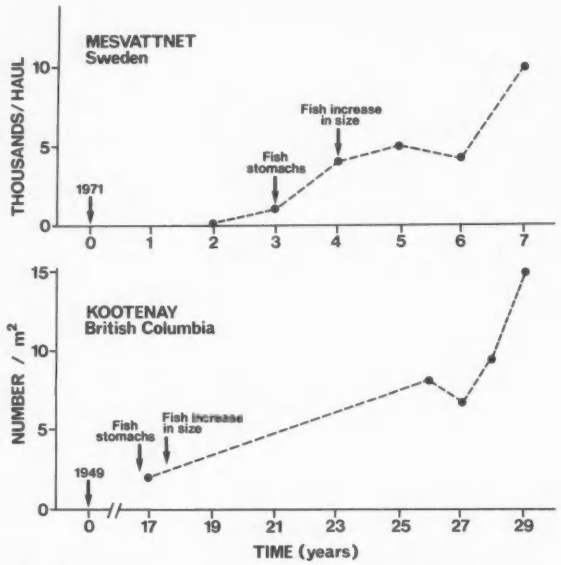

FIG. 3. Increases in *Mysis* density with time in Lake Mesvattnet, Sweden (modified from Olsén 1980), and Kootenay Lake, British Columbia (modified from Daley et al. 1981).

ponent of the diet of *Mysis* (see review by Grossnickle 1982). Often, however, both phytoplankton and zooplankton occur in the guts, making it impossible to determine if the phytoplankton came from the zooplankton or was directly ingested by the mysid. *Mysis* can filter a variety of sizes, shapes, and types of algal species from the water (D. C. Lasenby and D. R. S. Lean, in prep; Grossnickle 1979), "preferentially" ingest large filamentous algae (Bowers and Grossnickle 1978), and graze on laboratory-cultured diatoms (Sierszen and Brooks 1982). Long-term studies of the effect of *Mysis* introductions on the phytoplankton community of two small Swedish lakes (Kinsten and Olsén 1981) demonstrated that the mean summer phytoplankton biomass increased considerably in both lakes during the development of the *Mysis* populations. Kinsten and Olsén attributed the phytoplankton increase (mainly Cyanophyceae, Chrysophyceae, and Dinophyceae) to a decline in the cladoceran population after the mysid introduction, indicating that the effect of the *Mysis* was indirect.

Most of the recent research on *Mysis* feeding has centered on the predatory impact of *Mysis* on the zooplankton community. Reviews are provided by Grossnickle (1982) and Reiman and Falter (1981). The well-documented Lake Tahoe study (Richards et al. 1975; Morgan et al. 1978; and others) was the first to recognize the impact of *Mysis* on the zooplankton community. Two species of *Daphnia* and *Bosmina longirostris* disappeared from the main body of the lake in 1970. These changes were apparently the result of the introduction and growth in number of the planktivorous kokanee and *Mysis* as well as shifts in algal community structure (Byron et al. 1984). Although *Mysis* reaches a population maximum and minimum every 4 yr, the cladocerans reappear only when *Mysis* densities are low (Peter Sawyer, Tahoe Research Group, Division of Environmental Studies, University of California, Davis, CA, pers. comm.). Other studies since have reported similar declines in cladoceran populations following the introduction of *Mysis* (Daley et al. 1981; Langeland 1981; Reiman and Falter 1981). Reiman and Falter's study is particularly interesting, as they provided evidence that the mysids are not only responsible for the decline of cladocerans in Lake Pend Oreille, but also for the shifts in the dominance of daphnids from a round-helmet species (*Daphnia thorata*) to that with a sharply pointed helmet (*Daphnia galeata mendotae*). They also found a delayed summer appearance of both *Daphnia* species and *Bosmina longirostris*, possibly resulting from the isolation of the mysid population from the shallow water where the *Daphnia* lived during summer stratification.

The study by Kinsten and Olsén (1981) for small Swedish lakes provides one of the best documented cases of *Mysis* impact on the zooplankton community. In Lake Mesvattnet the composition of the zooplankton community changed dramatically after the increase in the *Mysis* population. The cladocerans, *Eubosmina longispina* and *Holopedium gibberum*, became almost extinct, and the rotifers have increased considerably. In Lake Mesvattnet, *Eubosmina* and *Holopedium* abundance decreased, rotifers increased, and the dominant cladoceran *Daphnia longispina* did not change. The copepod *Cyclops scutifer* remained unchanged in number although experiments demonstrated that *Mysis* readily fed on this species.

Effect on the Fish Communities

The first reported successful *Mysis* introduction in terms of the fish community was from the Kootenay Lake introduction. Here, the target species for growth enhancement was the rainbow trout. The population of large rainbow ("Gerrard stock") in the main lake did show increased growth rates between 1953 and 1959 compared with the period between 1943 and 1950 (Cartwright 1961). Length–weight relationships of Kootenay rainbow also suggested higher growth rates in the 1960's compared with the 1940's. However, over this same period the lake was undergoing eutrophication (Northcote 1972) and mysids did not form a major dietary component for any size class of these trout (Northcote 1973; Andrusak and Parkinson 1984). Thus, it was by no means clear that their introduction was responsible for the minor increase in growth rate observed because of the confounding effect of eutrophication.

On the other hand, there is little doubt that the mysid introduction was largely responsible for the remarkable increase in growth rate and size at maturity of some Kootenay Lake kokanee populations (Northcote 1973). Not only were 20–25 cm kokanee heavier in the mid-1960's than in the late 1940's, but a whole new size class of large fish (30–45 cm in length) appeared, some attaining weights of over 4 kg! Although a few large kokanee were found in the main lake (North and South arms), most were taken in the West Arm (outlet) portion of the lake. Here, in contrast with the other arms, *Mysis* was the dominant prey, especially for the large kokanee. Furthermore, total annual catch by anglers increased from a few hundred kokanee in the late 1940's, and early 1950's to about 100 000 in the early 1970's, largely a result of an intensive species specific fishery that developed in the West Arm.

Table 1 summarizes the information available for other British Columbia lakes into which *Mysis* has been introduced. The rainbow trout in some of these lakes have been reported to be utilizing *Mysis*, but there are no reported changes in rainbow trout growth and abundance. In general, follow-up work on the introductions, if it occurs at all, is not well documented.

In Lake Tahoe, the increase in the mysid population was related to a decline in the cladoceran population (Richards et al.

1975) and eventual collapse of the kokanee population. In the early 1970's, nearly 40 000 kokanee were spawning. In 1983, several hundred spawned (Peter Sawyer, pers. comm.). Lake trout length and catch per unit effort also declined. In Idaho and Montana lakes where *Mysis* was introduced, similar declines in kokanee have occurred (Rieman and Falter 1981; Reiman and Bowler 1980). However, enhanced survival and growth of juvenile lake trout following mysid introductions have been reported (Reiman and Lukens 1979; Griest 1977; Morgan et al. 1978) and briefly reviewed (Wydoski and Bennett 1981). Pygmy whitefish (*Prosopium coulteri*) and lake whitefish in Lake Pend Oreille, Idaho, also appear to benefit from mysids (Reiman and Falter 1981).

The lakes in Sweden into which *Mysis* has been introduced are mainly inhabited by salmonids such as brown trout and different sibling species of arctic char (*Salvelinus alpinus* species complex). These fish represent both littoral and hypolimnetic benthic feeders and pelagic plankton feeders. Detailed case studies of the effects of the *Mysis* introductions on the fish feeding habits have been made since 1966. The results show an increase in the number, growth, and quality of benthic fish, whereas the pelagic fish decrease in number (Fürst et al. 1986). The introduction of *Mysis* has been beneficial for brown trout, lake trout, and burbot in particular, and has also possibly favored benthic species of whitefish. *Mysis* has been shown to compete with pelagic populations of arctic char and whitefish for food. As a result of *Mysis* predation, several species of cladocerans have declined in abundance, and the pelagic fish, which normally feed on these, do not switch to a diet of *Mysis*. Consequently, these fish populations have declined in abundance (Fürst et al. 1986).

In impounded lakes where food is generally low for fish during winter, *Mysis* has become an important item in the fish diet. The arctic char from impounded lakes where *Mysis* has been introduced are of better quality than from impounded lakes without *Mysis*. The quality improves during the winter season, even after spawning (Fürst et al. 1984; Hill and Böstrom 1985).

In Swedish lakes with *Mysis* introductions, parasitism by the cestodes *Diphyllobothrium* spp. and *Triaenophorus* sp. has decreased in benthic fish species and increased in pelagic fish species. This may be explained by the observation that in the diet of the benthic fish, copepods, which serve as hosts for these parasites, have been replaced by *Mysis* as an important food item. On the other hand, copepods have become increasingly important in the diet of the pelagic fish, since *Mysis* has reduced the abundance of cladocerans (Hammar et al. 1983).

Discussion of Implications

Li and Moyle (1981) suggested a series of rules for use in fisheries management when introductions are being considered. Unfortunately one or more of these rules have been broken with most mysid introductions in North America and Scandinavia. For example, Li and Moyle stated that introductions should be considered mainly for systems that have been so altered by human activity that it is necessary to create a new community to take advantage of the change in production. Although mysids have been introduced into lakes which have been altered by human activity (reservoirs, cultural eutrophication), in many instances the lakes have been relatively unaltered. As well, Li and Moyle suggested that introductions should be considered mainly for isolated bodies of water so that uncontrolled spread of the introduced species is unlikely. In Scandinavia, it was expected that *Mysis* would move downstream, but introductions in North America have taken place without consideration of downstream dispersal of *Mysis*. In order to determine the intensity of the possible interactions between the introduced species and other species already present in the community, Li and Moyle indicated that studies that determine the species present in the community before the introduction should take place. With most mysid introductions, no "before" studies were carried out on any part of the aquatic community and very few "after" studies have been performed. Li and Moyle also suggested that introductions should not take place in oligotrophic lakes. Almost all *Mysis* introductions have occurred in such lakes. They suggested the following four criteria for a species that is being considered for an introduction: (1) the species should be part of a co-adapted trophic assemblage, with some members of the assemblage already being present within the system; (2) it would have a narrow niche breadth including being stenophagous; (3) it should have low vagility; (4) it should be free of contagious diseases and parasites exotic to the system.

As far as is known, most mysid introductions fulfill only one of these criteria. There are no reported cases of *Mysis* being introduced into lakes with serious consideration to the first criterion. With respect to the second criterion, *Mysis* certainly has a very broad niche breadth and is not stenophagous. Although recent research has concentrated on the predatory feeding of *Mysis*, its omnivory is well recognized. As well, the rapid downstream dispersal of *Mysis* in North American and Scandinavian watersheds indicates that it has quite high vagility. Although difficult to detect, there is no evidence that disease or parasites have been introduced along with mysids, but few serious attempts have been made to examine this possibility as far as we are aware. Fürst (1964) noted that although other glacial relict species in Scandinavia (e.g. *Pontoporeia*, *Pallasea*) may carry parasites, he found none in *Mysis*. These observations suggest that *Mysis* may not be a good candidate for further introductions to lakes as a fishery management practice.

At present, no methods are known for removing a *Mysis* population once it has been established in a lake. Also, very little is known about the impact of an introduced population on the lake community, although there are several documented examples of dramatic changes in the natural zooplankton assemblages in lakes receiving mysid introductions. There is little evidence that introductions are a positive long-term management practice and we agree with the recommendation of the Mysid Research Group (Morgan 1982) that until the probable impact of these introductions can be assessed (except for controlled research purposes) a moratorium should be imposed on further introductions of *Mysis relicta*.

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We would like to thank Mark Morgan for the original suggestion for this review. As well, we thank many of the fishery biologists in both the United States and Canada for their assistance in tracking down *Mysis* introductions. Special thanks to George Stringer, who provided much of the British Columbia data.

References

ANDRUSAK, H., AND E. PARKINSON. 1984. Food habits of the Gerrard stock rainbow trout in Kootenay Lake, British Columbia. B.C. Fish Wildl.

Branch Fish. Tech. Circ. No. 60: 14 p.

BERRILL, M., AND D. C. LASENBY. 1983. Life cycles of the freshwater mysid shrimp *Mysis relicta* reared at two temperatures. Trans. Am. Fish. Soc. 112: 551–553.

BOWERS, J. A., AND N. E. GROSSNICKLE. 1978. The herbivorous habits of *Mysis relicta* in Lake Michigan. Limnol. Oceanogr. 23: 767–776.

BYRON, E. R., C. L. FOLT, AND C. R. GOLDMAN. 1984. Copepod and cladoceran success in an oligotrophic lake. J. Plankton Res. 6: 45–65.

CARTWRIGHT, J. W. 1961. Investigation of the rainbow trout of Kootenay Lake, British Columbia with special reference to the Lardeau River. B.C. Fish Wildl. Branch Fish. Manage. Publ. No. 7: 46 p.

CLEMENS, W. A., D. S. RAWSON, AND J. L. MCHUGH. 1939. A biological survey of Okanagan Lake, British Columbia. Bull. Fish. Res. Board Can. 56: 70 p.

DADSWELL, M. J. 1974. Distribution ecology and postglacial dispersal of certain crustaceans and fishes in eastern North America. Publ. Zool. Nat. Mus. Nat. Sci. (Ottawa) (11): 110 p.

DALEY, R. J., E. C. CARMACK, C. B. J. GRAY, C. H. PHARO, S. JASPER, AND R. C. WIEGAND. 1981. The effects of upstream impoundments on the limnology of Kootenay Lake, B.C. Nat. Water Res. Inst. Sci. Ser. No. 117: 98 p.

DRYER, W. R., L. F. ERKKILA, AND C. L. TETZLOFF. 1965. Food of the lake trout in Lake Superior. Trans. Am. Fish. Soc. 194: 169–176.

EVANS, R. D., AND D. C. LASENBY. 1983. Relationship between body-lead concentration of *Mysis relicta* and sediment-lead concentration in Kootenay Lake, B.C. Can. J. Fish. Aquat. Sci. 40: 78–81.

FÜRST, M. 1964. Glacial relict crustaceans as hosts for fish parasites. Inf. Sötvattens–Laboratoriet, Drottningholm 10: 5 p. (In Swedish)

1972a. Experiments on the transplantation of new fish-food organisms into Swedish impounded lakes. The feeding habits of brown trout and char in Lake Blåsjön. Int. Ver. Theor. Angew. Limnol. 18: 1114–1121.

1972b. Life cycles, growth and reproduction in *Mysis relicta* Lovén. Inf. Sötvattens–Laboratoriet, Drottningholm 11: 41 p. (In Swedish with English summary)

1981. Results of introductions of new fish food organisms into Swedish lakes. Inst. Freshwater Res. Drottningholm 59: 33–47.

FÜRST, M., V. BÖSTROM, AND J. HAMMAR. 1978. Effects of new fish-food organisms in Lake Blaåsjön. Inf. Sötvattens–Laboratoriet, Drottningholm 15: 95 p. (In Swedish with English summary)

FÜRST, M., J. HAMMAR, AND C. HILL. 1986. The introduction of *Mysis relicta* in Sweden: effects on fish species in impounded lakes. EIFAC Symposium on Habitat Modification and Freshwater Fisheries, Aarhus, Denmark.

FÜRST, M., J. HAMMAR, C. HILL, U. BÖSTROM, AND B. KINSTEN. 1984. Effects of the introduction of *Mysis relicta* into impounded lakes in Sweden. Inf. Sötvattens–Laboratoriet, Drottningholm 1: 84 p. (In Swedish with English summary)

GOSHO, M. 1975. The introduction of *Mysis relicta* into freshwater lakes. Fisheries Research Institute, University of Washington, Seattle, WA. 75–2: 66 p.

GRIEST, T. R. 1977. The lake trout of Twin Lakes, Colorado. United States Bureau of Reclaimation Report REC-ERC-77-4, Denver, CO.

GRIMÅS, U. 1961. The bottom fauna of natural and impounded lakes in northern Sweden. (Ankarvattnet and Blåjön). Inst. Freshwater Res. Drottningholm 42: 183–237.

GROSSNICKLE, N. E. 1979. Nocturnal feeding patterns of *Mysis relicta* in Lake Michigan, based on gut content fluorescence. Limnol. Oceanogr. 24: 778–780.

1982. Feeding habits of *Mysis relicta* — an overview, p. 101–108. *In* M. D. Morgan [ed.] Ecology of Mysidacea. W. Junk Publ., The Hague, The Netherlands.

GROSSNICKLE, N. E., AND M. B. MORGAN. 1979. Density estimates of *Mysis relicta* in Lake Michigan. J. Fish. Res. Board Can. 36: 694–698.

HAMMAR, J., O. LINDH, U. BÖSTROM, F. FÜRST, AND P. LINGDELL. 1983. The arctic char and *Diphyllobothrium* spp. Control of infection by means of the introduction of *Mysis relicta* as a new and alternative fish food organism. Inf. Sötvattens–Laboratoriet, Drottningholm 4: 72 p. (In Swedish with English summary)

HANSEN, J. A. 1966. The final introduction of the opossum shrimp (*Mysis relicta*) into California and Nevada. Calif. Fish Game 52: 220.

HILL, C., AND U. BÖSTROM. 1985. Effects of the introduction of *Mysis relicta* on the quality of arctic char. Inf. Sötvattens–Laboratoriet, Drottningholm 3: 54 p. (In Swedish with English summary)

KINSTEN, B., AND P. OLSÉN. 1981. Impact of *Mysis relicta* introduction on the plankton of two mountain lakes, Sweden. Inst. Freshwater Res. Drottningholm 59: 64–74.

LANGELAND, A. 1981. Decreased zooplankton density in two Norwegian lakes caused by predation of recently introduced *Mysis relicta*. Int. Ver. Theor. Angew. Limnol. 21: 926–937.

LARKIN, P. A. 1951. Summary of investigation conducted by the Fisheries Research Group, attached to the British Columbia Game Department, in 1949. Annual Report of the British Columbia Game Commission for 1949. p. 55–61.

1952. The role of research in the management of freshwater fisheries in British Columbia. Can. Fish-Cult. 12: 10–12.

LASENBY, D. C. 1971. The ecology of *Mysis relicta* in an arctic and a temperate lake. Ph.D. thesis, University of Toronto, Toronto, Ont. 119 p.

LASENBY, D. C., AND M. FÜRST. 1981. Feeding of *Mysis relicta* Lovén on macrozooplankton. Inst. Freshwater Res. Drottningholm 59: 75–80.

LASENBY, D. C., AND R. R. LANGFORD. 1973. Feeding and assimilation of *Mysis relicta*. Limnol. Oceanogr. 18: 280–285.

LI, H. W., AND P. B. MOYLE. 1981. Ecological analysis of species introductions into aquatic systems. Trans. Am. Fish. Soc. 110: 772–782.

LINN, J. D., AND T. C. FRANTZ. 1965. Introduction of the opossum shrimp (*Mysis relicta* Lovén) in California and Nevada. Calif. Fish Game 51: 48–51.

MORGAN, M. D. 1981. Abundance, life history, and growth of introduced populations of the opossum shrimp (*Mysis relicta*) in subalpine California lakes. Can. J. Fish. Aquat. Sci. 38: 989–993.

MORGAN, M. D. [ED.] 1982. Ecology of Mysidacea. W. Junk Publ., The Hague, The Netherlands. 222 p.

MORGAN, M. D., S. T. THRELKELD, AND C. R. GOLDMAN. 1978. Impact of the introduction of kokanee and opossum shrimp on a subalpine lake. J. Fish. Res. Board Can. 35: 1572–1579.

NERO, R. W., AND I. J. DAVIES. 1982. Comparison of two sampling methods for estimating the abundance and distribution of *Mysis relicta*. Can. J. Fish. Aquat. Sci. 39: 349–355. .

NORTHCOTE, T. G. 1970. Advances in management of fish in natural lakes of western North America, p. 129–139. *In* N. G. Benson [ed.] A century of fisheries in North America. Am. Fish. Soc. Spec. Publ. 7: 330 p.

1972. Some effects of mysid introduction and nutrient enrichment on an oligotrophic lake and its salmonids. Int. Ver. Theor. Angew. Limnol. 18: 1096–1106.

1973. Some impacts of man on Kootenay Lake and its salmonids. Great Lakes Fish. Comm. Tech. Rep. No. 25: 46 p.

OLSÉN, P. 1980. The population of *Mysis relicta* after introduction in two mountain lakes, Sweden. Scr. Limnol. Upsaliensia 504: 41 p.

PARKER, J. I. 1980. Predation by *Mysis relicta* on *Pontoporeia hoyi*: a food chain link of potential importance in the Great Lakes. Int. Assoc. Great Lakes Res. 6(2): 164–166.

RICHARDS, R. C., C. R. GOLDMAN, T. C. FRANTZ, AND R. WICKWIRE. 1975. Where have all the *Daphnia* gone? The decline of a major cladoceran in Lake Tahoe, California–Nevada. Int. Ver. Theor. Angew. Limnol. 19: 835–842.

RIEMAN, B. E., AND B. BOWLER. 1980. Trophic ecology of kokanee and limnology in Pend Oreille Lake. Idaho Fish and Game Fisheries Bulletin 1, Boise, ID.

RIEMAN, B. E., AND C. M. FALTER. 1981. Effects of the establishment of *Mysis relicta* on the macrozooplankton of a large lake. Trans. Am. Fish. Soc. 110: 613–620.

RIEMAN, B. E., AND J. R. LUKENS. 1979. Priest Lake creel census. Idaho Fish and Game Lake and Reservoir Investigations, Job Completion Report F-73-R-1, Boise, ID.

ROBERTSON, A., C. F. POWERS, AND R. F. ANDERSON. 1968. Direct observations on *Mysis relicta* from a submarine. Limnol. Oceanogr. 13: 700–702.

SIERSZEN, M. E., AND A. S. BROOKS. 1982. The release of dissolved organic carbon as a result of diatom fragmentation during feeding by *Mysis relicta*, p. 115–162. *In* M. D. Morgan [ed.] Ecology of Mysidacea. W. Junk Publ., The Hague, The Netherlands.

SPARROW, R. A. H., P. A. LARKIN, AND R. A. RUTHERGLEN. 1964. Successful introduction of *Mysis relicta* Lovén into Kootenay Lake, British Columbia. J. Fish. Res. Board Can. 21: 1325–1327.

STRINGER, G. E. 1967. Introductions of *Mysis relicta* Lovén into Kalamalka and Pinaus Lakes, British Columbia. J. Fish. Res. Board Can. 24: 463–465.

WELLS, L., AND A. M. BEETON. 1963. Food of the bloater, *Coregonus hoyi*, in Lake Michigan. Trans. Am. Fish. Soc. 92: 245–255.

WETZEL, R. G. 1983. Limnology. Saunders, Toronto, Ont. 110 p.

WYDOSKI, R. S., AND D. H. BENNETT. 1981. Forage species in lakes and reservoirs of the western United States, Trans. Am. Fish. Soc. 110: 764–771.

NOTES

Influence of pH, Aluminum, and Organic Matter on Stream Invertebrates[1]

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The interactive effects of low pH, aluminum, and organic matter on five species of invertebrates collected from low-alkalinity (160–300 μeq/L) Michigan streams were measured using five 28-d experiments during 1982 and 1983. Such interactive effects had not been tested previously for these species. Each experiment consisted of a control channel (pH 7.0), a pH modified (4.0 or 5.0), and pH plus Al (250 or 500 μg Al/L) modified channel. Three experiments were conducted using natural stream water (dissolved organic carbon of 42–47 mg C/L), while two were conducted using simulated stream water with no dissolved organic carbon added. The invertebrates included *Asellus intermedius* Forbes, *Pycnopsyche guttifer* (Walker), *Lepidostoma liba* (Ross), *Nemoura* sp., and *Physella heterostropha* (Say). Survival of all species was significantly decreased at pH 4 compared with controls but not at pH 5 except for *Asellus* (15–20% mortality). Adding 500 μg Al/L caused significant additional mortality under some conditions for all species except *Physella*. Removal of organic matter from the water caused complete mortality at pH 4 for *Nemoura* and *Asellus* when 500 μg Al/L was added and decreased survival for *Pycnopsyche* to less than 20%. Addition of citrate as an organic ligand reduced susceptibility to Al in the low-organic streamwater treatment.

En 1982 et 1983, on a mesuré les effets interactifs d'un faible pH, de l'aluminium et de la matière organique sur cinq espèces d'invertébrés recueillis dans des cours d'eau du Michigan de faible alcalinité (160–300 μeq/L) en réalisant cinq expériences de 28 jours. Ces effets interactifs n'ont pas été vérifiés précédemment pour ces espèces. Chaque expérience comprenait un chenal témoin (pH de 7,0), un chenal à pH modifié (4,0 ou 5,0) et un chenal à pH modifié plus l'Al (250 ou 500 μg/L d'Al). Trois expériences ont été faites en utilisant de l'eau venant de cours d'eau naturels (carbone organique dissous de 42 à 47 mg/L de C) alors que deux l'ont été en utilisant de l'eau provenant de cours d'eau simulés à laquelle on n'avait pas ajouté de carbone organique dissous. Parmi les invertébrés, on retrouvait *Asellus intermedius* Forbes, *Pycnopsyche guttifer* (Walker), *Lepidostoma liba* (Ross), *Nemoura* sp. et *Physella heterostropha* (Say). Il y a eu une baisse importante du taux de survie chez toutes les espèces à un pH de 4 par rapport aux témoins mais pas à un pH de 5, sauf pour *Asellus* (15 à 20 % de mortalité). L'ajout de 500 μg/L d'Al a provoqué dans certaines conditions un taux de mortalité additionnel important pour toutes les espèces à l'exception de *Physella*. Suite à l'enlèvement de la matière organique de l'eau, il y a eu une mortalité de 100 % à un pH de 4 pour *Nemoura* et *Asellus* lorsqu'on ajoutait 500 μg/L d'Al et une baisse du taux de survie pour *Pycnopsyche* à moins de 20 %. L'addition de citrate comme ligand organique a réduit la sensibilité à l'aluminium dans les conditions expérimentales où l'eau avait une faible teneur en matière organique.

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Acidification causes increased mortality for many species of stream invertebrates (Bell and Nebeker 1969; Roback and Richardson 1969; Bell 1971; Herricks and Cairns 1974; Fiance 1978; Hall and Likens 1980; Hall et al. 1980; Arnold et al. 1981; Haines 1981; Raddum and Steigen 1981; Zischke et al. 1983; Cook and Haney 1984).

The elevated levels of aluminum that accompany acidification may increase susceptibility of invertebrates to acidification (Raddum 1980; Harriman and Morrison 1982; Havas and Hutchinson 1982; Otto and Svensson 1983; Cook and Haney 1984; Hall et al. 1985). Complexation of Al with humic

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substances may alter its speciation, distribution, and toxicity (Dickson 1978; Driscoll et al. 1980). Thus, the interaction of pH, Al, and organic matter may determine the impact of acidification on stream biota. These interactive effects have been studied for only a few fish (Driscoll et al. 1980; Henriksen et al. 1984). No study varying all three factors has been done for invertebrates, although field correlations have suggested the importance of these interactions (Otto and Svensson 1983). The objective of this research was to determine the interactive effects of low pH, Al, and organic matter on five species of stream invertebrates.

Materials and Methods

Experimental design — Five 28-d experiments were conducted in 1982 and 1983 on a snail, *Physella heterostropha* (Say); an isopod, *Asellus intermedius* Forbes; two species of caddisflies, *Lepidostoma liba* (Ross) and *Pycnopsyche guttifer* (Walker); and a stonefly, *Nemoura sp.* Latreille. All five species were collected from two circumneutral (pH 6.7−7.2), low-alkalinity (160−300 μeq/L), first-order reference streams in Chippewa County, Michigan (T49N, R6W, Sec 15) and were acclimated to conditions in indoor laboratory streams for 2−4 wk prior to experimentation. Since invertebrates were collected prior to each experiment, life stage tested varied depending on the time of year the experiment was conducted.

The laboratory streams in four of the experiments consisted of three 2.1-m-long × 0.6-m-wide × 0.56-m-deep recirculating, temperature-controlled channels. Water depth was maintained at 20 cm in each stream. Experiment 3 in this series was conducted in slightly larger recirculating stream channels. These larger streams had no refrigeration units as did streams in the other experiments, but water temperature was controlled to ±3° by circulating cool water through tygon tubing in the channels. Photoperiod was controlled in all five experiments to simulate field conditions and was adjusted seasonally based on sunrise−sunset data for East Lansing, Michigan.

For each experiment, each species of invertebrate was placed in 15 × 10 × 6 cm cages consisting of a Plexiglas frame covered with 1-mm-mesh nylon netting. Ten grams of dried birch leaves, *Betula papyrifera*, collected from the forest floor near the reference streams at time of leaf fall the previous autumn, was placed in each cage. These leaves were dried at 60°C, stored until time of use, and redried and weighed before use. After 2 wk of conditioning and preleaching in natural stream water, the leaves were placed in cages in the experimental streams for 2 wk prior to addition of invertebrates for acclimation. Three cages of 20 invertebrates per species for four of the species were placed in each stream (i.e. 60 individuals per species per stream). For *Asellus*, 40 individuals per cage per stream or 120 individuals per stream were used in the experiments. After acclimation, experiments were initiated by adding 70% H_2SO_4/30% HNO_3 and appropriate amounts of $AlCl_3$ over a 6-h period to attain the acidity and Al levels desired. pH was tested and adjusted daily to the desired level. Few changes occurred so few adjustments were needed. Dissolved organic carbon (DOC) was not measured after acidification but no color change was apparent suggesting no major drop in DOC. The 250 or 500 μg Al/L added was within the range of 200−1000 μg Al/L reported for many acidified lakes and streams (Hendrey 1981).

In experiments E1 and E2, natural stream water (42−47 mg DOC/L) was collected during collection of invertebrates and introduced into the laboratory streams. One laboratory stream was maintained at the pH of the natural streams (6.8−7.2) as a control; the second was acidified to pH 4.0 (4.0−4.2); and the third channel was acidified to pH 4.0 also but 500 μg Al/L was added as well. Experiment E1 was conducted in August at 15°C, the average August temperature of the natural streams, while experiment E2 was conducted in January at 2°C.

Experiment E3 was conducted in August at the same time as E1 using deionized water with the inorganic chemistry adjusted to simulate mean annual natural stream concentrations (Burton et al. 1982). This experiment repeated E1 except that no organic matter was present other than amounts introduced with leaf packs and invertebrates used in the experiment, and temperature was 5−8° higher. Experiment E4 was similar to E3 except that Al was introduced as an alumino-organic (citrate) ligand following the procedures of Driscoll et al. (1980), and the experiment was conducted in September−October at 12°C.

Experiment E5 was conducted using natural streamwater during November−December at 2°C. However, pH was only lowered to 5.0 and only 250 μg Al/L was added. Other than these changes, this experiment was similar to the midwinter natural stream water experiment (E2, 2°C).

Statistical comparisons were made on percent survival data after arcsin square root transformations as recommended by Steel and Torrie (1960). Results from experiments E1−E4 which were acidified to pH 4 were compared using a three-way ANOVA with replication. Significant interactions from this ANOVA were compared with Tukey's *W* pairwise comparison technique (Steel and Torrie 1960). Results from experiment E5 (acidified to pH 5) were analyzed using a two-way ANOVA plus Tukey's *W* test. Some within-experiment comparisons were made using one-way ANOVA's and/or Students *t*-test. Results were deemed significant at $p < 0.05$.

Analytical procedures — Metals concentrations were determined with an inductively coupled plasma emission spectrophotometer by the Animal Health Diagnostic Laboratory at Michigan State University. NO_3-N, NO_2-N, NH_4-N, total N, soluble reactive P, total P, Cl, hardness, and alkalinity were analyzed using automated, autoanalyzer techniques (U.S. EPA 1979). Sulfate was determined by the turbidimetric method, fluoride by the SPANDS method, and dissolved oxygen by the azide modification of the Winkler test (APHA 1975). pH was measured with pH meters calibrated with pH 4 and 7 buffers. Aluminum speciation was evaluated using the techniques of Rainwater and Thatcher (1960) with modifications proposed by Driscoll (1980, 1984).

Results and Discussion

Chemical responses — Changes in chemistry other than the experimental modification of pH and Al occurred. Acidification resulted in increases in organic N from 0.43−0.71 mg N/L initially and in the controls to 1.93−3.05 in the pH 4 treatments in E1 and E2 and to 1.41−1.52 in the pH 4 treatments for E5. NO_3-N increased also from 0.29−0.31 initially and in controls in E1 to 1.48−1.53 in the acidified treatments, from 0.31−0.42 to 3.14−4.28 in E2, and from 0.20−0.24 to 1.39−1.49 in E5. E3 and E4 had similar increases from initial to final values. However, control values also increased (from 0.28 to 1.14 in E3 and 0.32 to 0.99 in E4 for NO_3-N and from 0.34 to 1.72 for E3 and 0.47 to 1.35 for organic N). The reason for this increase could include increased leaching of leaf material, increased invertebrate excretion, or could be related

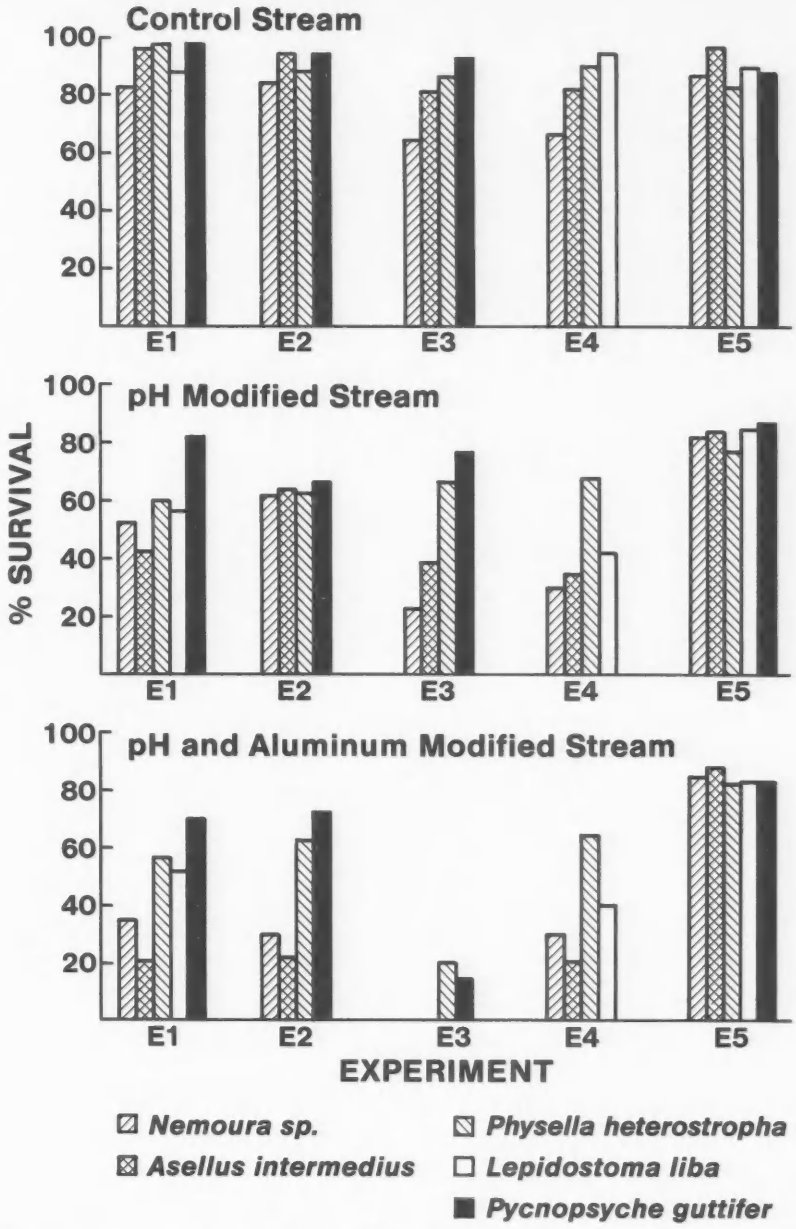

FIG. 1. Percent survival of invertebrates in experiments E1–E5. In E1–E4, pH was reduced from 7.0 to 4.0 and 500 μg Al/L was added; in E5, pH was reduced from 7.0 to 5.0 and 250 μg Al/L was added.

to the deionization process. Fluoride also differed between the natural stream water experiments and the inorganic simulated stream water experiments with a decrease from a mean concentration of 0.73 mg F/L in the former (E1, E2, and E5) to less than 0.01 in the latter (E3 and E4). Other than these changes and increases in SO_4 due to additions during acidification, no significant differences were detected for any other constituents between the acidified and control treatments.

In the natural stream water experiments (E1, E2, and E5), about two thirds of total Al existed as organically bound Al with the remaining one third existing as inorganic Al. The organic fraction was composed of 80–90% monomeric Al, while the remaining 10–20% existed as polymeric compounds. The reduction in pH had only slight effects on the percent contribution of each fraction of organically bound Al. Thus, no significant difference existed in Al speciation between experiments E1, E2, and E5.

Removal of organic matter from stream water resulted in an

almost complete (94–98%) shift to inorganic forms of Al as expected in the experimental design. Addition of citrate as an organic ligand in E3 shifted Al speciation back towards organically complexed forms, with 81% of Al existing in this form.

Biotic responses — Survival of all five species differed markedly between experiments and treatments (Fig. 1). Because of pupation and/or emergence during some of the experiments, not all experiments included *Lepidostoma* or *Pycnopsyche*. Thus, a three-way ANOVA with replication was used to compare data for *Nemoura*, *Asellus*, and *Physella* for all four experiments acidified to pH 4 (E1–E4, Fig. 1). For these species, there were significant differences between experiments, treatments, and species and significant interactions between experiment and treatment, experiment and species, and treatment and species. The three-way interaction between experiment, treatment, and species was not significant.

In experiment E1 (natural stream water, 15°C), acidification to pH 4 resulted in significant mortality for all three species as did acidification to pH 4 with 500 μg Al/L added (Fig. 1). However, differences between the pH 4 stream and pH 4 plus 500 μg Al/L stream (Fig. 1) were not significant.

Experiment E2 (natural stream water, 2°C) differed from E1 in season and temperature (August at 15°C, January at 2°C) and in life stage tested. Results for *Nemoura*, *Asellus*, and *Physella* were similar to results from E1, with significant mortality occurring in the pH 4 stream and the pH 4 plus 500 μg Al/L stream (Fig. 1). However, the addition of 500 μg Al/L resulted in significant additional mortality for *Nemoura* and *Asellus* in this experiment (Fig. 1). No significant additional mortality occurred for *Physella* when 500 μg Al/L was added to the pH 4 conditions. The significant added mortality in January for *Asellus* was noteworthy because it occurred despite the fact that the larger (3.8 mg dry wt.) January E2 individuals have been demonstrated to be significantly less susceptible to pH 4 conditions than are smaller (0.5 mg dry wt.) El August individuals (Allan and Burton 1986). This trend of lower susceptibility of larger individuals appeared to be true for experiments E1 and E2 (Fig. 1), with higher survival rates for pH 4 treatment in E2 compared with E1, although differences were not significant. The significant added mortality of larger individuals at 4°C due to Al additions suggests either that susceptibility to Al toxicity increases with size (opposite the trend for pH) or that lower temperatures increase this susceptibility.

In experiment E3 with little or no organic matter present, acidification to pH 4 resulted in significant mortality for *Nemoura*, *Asellus*, and *Physella*, while acidification plus 500 μg Al/L resulted in significant additional mortality over acidification to pH 4 for both *Nemoura* and *Asellus* but not for *Physella* (Fig. 1). In fact, survival was zero for both *Nemoura* and *Asellus* at pH 4 with 500 μg Al/L added. Fewer specimens of *Physella* survived but these differences were not significant using Tukey's *W* test. A *t*-test comparison of these data did show a significant difference resulting from Al additions for *Physella*.

In experiment E4, the only organic matter present was citrate added to the pH 4 plus 500 μg Al/L treatment as an organic ligand. Again, acidification to pH 4 or to pH 4 with 500 μg Al/L added resulted in significant mortality compared with the control (Fig. 1). The addition of 500 μg Al/L to pH 4 conditions resulted in significant additional mortality compared with pH 4 conditions alone for *Asellus* but not for the other two species. These results were similar to results from E1 and E2, the natural stream water experiments (Fig. 1).

Within each experiment, acidification to pH 4 with no added Al resulted in significant mortality for all three species as did acidification to pH 4 with Al (Fig. 1). The added Al caused additional significant mortality for *Nemoura* in E2 and E3 but not in E1 or E4, for *Asellus* in E2, E3, and E4 but not in E1, and for *Physella* in none of the four experiments using Tukey's *W* comparison (significant additional mortality was indicated in E3 using a *t*-test comparison).

Pairwise comparison of mortality from experiment to experiment for both control and pH 4 conditions demonstrated that *Nemoura* had greater survival in natural stream water (E1 and E2, Fig. 1) than in low organic water (E3 and E4). This trend was also true for pH 4 plus 500 μg Al/L conditions when E1 or E2 was compared with E3. However, addition of citrate to E4 resulted in survival increasing for the pH 4 plus Al conditions to levels not significantly different from E1 and E2 (Fig. 1).

For *Asellus*, the only differences in survival for controls between experiments occurred for E1 versus E3 or E4 (Fig. 1). These differences disappeared when E2 was compared with E3 or E4. Thus, there was a suggestion that low organic content of water decreased survival for this species but the relationship was not consistent for all comparisons as it was for *Nemoura*. In the stream acidified to pH 4, there were no significant differences in survival between any pair of experiments except when E2 was compared with E3. When 500 μg Al/L was added, survival of *Asellus* was significantly different for E3 (no organic present) compared with any of the other experiments but no other differences existed between any other experiments.

A comparison of percent survival for the three species between experiments showed that *Asellus* and *Nemoura* always had lower survivorship when exposed to acidification to pH 4 or to pH 4 plus 500 μg Al/L than did *Physella*. The responses of *Nemoura* and *Asellus* to treatments were very similar with little difference between the two species. All three species were susceptible to pH 4 and to pH 4 plus 500 μg Al/L, but *Nemoura* and *Asellus* were much more susceptible than was *Physella* (Fig. 1).

Pycnopsyche guttifer emerged during experiment E4. A two-way ANOVA for E1, E2, and E3 demonstrated that there were significant effects of experiment, treatment, and experiment–treatment interactions for this species. One-way ANOVA within experiments showed that acidification to pH 4 with or without Al caused significant mortality for E1 and E2 but not E3 (Fig. 1). One-way ANOVA's comparing percent survival within experiments for pH 4 conditions to pH 4 plus 500 μg Al/L conditions showed that significant additional mortality due to Al addition occurred for E1 and E3 but not for E2 (Fig. 1). Survival was lower in the low organic content water (E3) than in the natural stream water when 500 μg Al/L was added (Fig. 1).

Lepidostoma liba was only included in experiments E1 and E4 in the pH 4 acidification treatments (E1 and E4, Fig. 1). A two-way ANOVA comparing these two experiments showed that treatment effects were significant but that differences between experiments and treatment–experiment interactions were not significant. In both experiments, acidification with or without added Al caused significant mortality compared with controls (one-way ANOVA) but the 500 μg Al/L did not cause additional significant mortality over the pH 4 treatment alone

(Fig. 1).

Experiment E5 was similar to experiment E4 (natural stream water at 2°C during winter) except that acidification was only to pH 5 and only 250 μg Al/L was added to the third treatment. All five species were included in experiment E5. A two-way ANOVA of E5 showed that there were significant effects of both species and treatment but that interaction between species and treatment was not significant. Pairwise comparisons between means showed that there were no significant differences between survival in the control and in the pH 5 or pH 5 plus 250 μg Al/L channels for *Nemoura, Physella, Pycnopsyche,* and *Lepidostoma* (Fig. 1). For *Asellus*, acidification to pH 5 caused a slight but significant increase in mortality. Addition of 250 μg Al/L to pH 5 conditions caused no added mortality over pH 5 conditions alone for any of the five species. In fact, percent survival in the pH 5 plus 250 μg Al/L conditions was only significantly different for *Asellus* from the control at the $p < 0.1$ level.

These results suggest that the interactive effects between pH, Al, and organic matter are important in determining susceptibility of invertebrates to acidification. Decreasing pH to 4.0 from 7.0 caused significant mortality for all species studied. Addition of 500 μg Al/L caused additional mortality for some species but not all. The toxicity of this Al appeared to be influenced by the organic content of water through its influence on Al speciation. High percentages of monomeric Al appeared to increase mortality, especially for *Asellus* and *Nemoura*. Monomeric Al only existed as a high percentage of total Al in the low organic content stream water.

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References

ALLAN, J. W., AND T. M. BURTON. 1986. Size dependent sensitivity of three species of stream invertebrates to pH depression. *In* Proceedings of a Symposium on Impact of Acid Rain and Deposition on Aquatic Biological Systems. ASTM, Philadelphia, PA. (In press).

APHA 1975. Standard methods for the examination of water and wastewater. 14th ed. American Public Health Association, Washington, DC.

ARNOLD, D. E., P. M. BENDER, A. B. HALE, AND R. W. LIGHT. 1981. Studies on infertile, acidic Pennsylvania streams and their benthic communities, p. 15–33. *In* R. Singer [ed.] Effects of acidic precipitation on benthos. North American Benthological Society, Environmental Protection Agency, Springfield, IL.

BELL, H. 1971. Effects of low pH on the survival and emergence of aquatic insects. Water Res. 5: 313–319.

BELL, H., AND A. NEBEKER. 1969. Preliminary studies on the tolerance of aquatic insects to low pH. J. Kans. Entomol. Soc. 42: 230–236.

BURTON, T. M., R. M. STANFORD, AND J. W. ALLAN. 1982. Chapter 9. The effects of acidification on stream ecosystems, p. 209–235. *In* F. M. D'Itri [ed.] Acid precipitation: effects on ecological systems. Ann Arbor Science Publishers, Ann Arbor, MI.

COOK, W., AND J. HANEY. 1984. The acute effects of aluminum and acidity upon nine stream insects. Res. Rep. 46, Water Resource Research Center, Durham, NH. 33 p. 10 figs.

DICKSON, W. 1978. Some effects of the acidification of Swedish lakes. Verh. Int. Ver. Limnol. 20: 851–856.

DRISCOLL, C. T. 1980. Chemical characterization of some dilute acidified lakes and streams in the Adirondack Region of New York State. Ph.D. thesis, Cornell University, Ithaca, NY. University Microfilms International, Ann Arbor, MI.

1984. A procedure for the fractionation of aqueous aluminum in dilute acidic waters. Int. J. Environ. Anal. Chem. 16: 267–284.

DRISCOLL, C. T., J. P. BAKER, J. J. BISOGNI, AND C. L. SCHOFIELD. 1980. Effect of aluminum speciation on fish in dilute acidified waters. Nature (Lond.) 284: 161–164.

FIANCE, S. B. 1978. Effects of pH on the biology and distribution of *Ephemerella funeralis* (Ephemeroptera). Oikos 31: 332–339.

HAINES, T. A. 1981. Acid precipitation and its consequences for aquatic ecosystems: a review. Trans. Am. Fish. Soc. 110: 669–707.

HALL, R. J., C. T. DRISCOLL, AND G. E. LIKENS. 1985. Physical, chemical, and biological consequences of episodic aluminum additions to a stream system. Limnol. Oceanogr. 30(1): 212–220.

HALL, R. J., AND G. E. LIKENS. 1980. Ecological effects of experimental acidification on stream ecosystems, p. 375–376. *In* D. Drablos and A. Tollan [ed.] Ecological impact of acid precipitation. Proc. Int. Conf., Sandefjord, Norway.

HALL, R. J., G. E. LIKENS, S. B. FIANCE, AND G. R. HENDREY. 1980. Experimental acidification of a stream in the Hubbard Brook Experimental Forest, New Hampshire. Ecology 61(4): 976–989.

HARRIMAN, R., AND B. R. S. MORRISON. 1982. Ecology of streams draining forested and non-forested catchments in an area of Scotland subject to acid precipitation. Hydrobiologia 88: 251–263.

HAVAS, M., AND T. C. HUTCHINSON. 1982. Aquatic invertebrates from the Smoking Hills, N.W.T.: effect of pH and metals on mortality. Can. J. Fish. Aquat. Sci. 39: 890–903.

HENDREY, G. R. 1981. Acid rain and gray snow. Nat. Hist. 90(2): 58–64.

HENRIKSEN, A., O. K. SKOGHEIM, AND B. O. ROSSELAND. 1984. Episodic changes in pH and aluminum-speciation kill fish in a Norwegian salmon river. Vatten 40: 255–260.

HERRICKS, E. E., AND J. CAIRNS, JR. 1974. The recovery of stream macrobenthos from low pH stress. Rev. Biol. 10(1–4): 1–11.

OTTO, C., AND B. S. SVENSSON. 1983. Properties of acid brown water streams in South Sweden. Arch. Hydrobiol. 99(1): 15–36.

RADDUM, G. 1980. Comparison of benthic invertebrates in lakes with different acidity, p. 330–331. *In* D. Drablos and A. Tollan [ed.] Ecological impact of acid precipitation. Proc. Int. Conf., Sandefjord, Norway.

RADDUM, G. E., AND A. L. STEIGEN. 1981. Reduced survival and control of stoneflies and caddisflies in acidic water, p. 97–101. *In* R. Singer [ed.]. Effects of acidic precipitation on benthos. North American Benthological Society, Environmental Protection Agency, Springfield, IL.

RAINWATER, F. J., AND L. L. THATCHER. 1960. Methods for collection and analysis of water samples. U.S. Geol. Surv. Water-Supply Pap. 1454.

ROBACK, S. S., AND J. W. RICHARDSON. 1969. The effects of acid mine drainage on aquatic insects. Proc. Acad. Nat. Sci. Phila. 121: 81–107.

STEEL, R. G. D., AND J. H. TORRIE. 1960. Principles and procedures of statistics. McGraw-Hill Book Co., Inc., New York, NY. 481 p.

U.S. EPA. 1979. Methods for chemical analysis of water and wastes. EPA-600/479–020, U.S. Environmental Protection Agency, Cincinnati, OH.

ZISCHKE, J. A., J. W. ARTHUR, K. J. NORDLIE, R. O. HERMANUTZ, D. A. STANDEN, AND T. P. HENRY. 1983. Acidification effects on macroinvertebrates and fathead minnows (*Pimephales promelas*) in outdoor experimental channels. Water Res. 17: 47–63.

Patterns and Rates of Ammonia Excretion by Juvenile American Lobsters, *Homarus americanus*, Fed Casein- and Crab Protein-Based Diets

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The rate of excretion of nitrogenous wastes is not only a function of an animal's metabolic status but is also a function of the nutritional quality and quantity of dietary protein. Hourly rates of ammonia excretion by Stage V and Stage VI juvenile lobsters, *Homarus americanus*, fed purified diets formulated with casein or a purified crab protein, were measured over 24 h postfeeding to evaluate differences in use efficiencies of these two dietary proteins. Hourly ammonia excretion rates by Stages V and VI lobsters fed the casein-based formulated diets were significantly higher than those of animals fed the crab protein formulation. In addition to differences in ammonia excretion rates observed between animals fed the two diets, regular but different recurring patterns in hourly excretion rates were found between Stages V and VI lobsters fed each diet. Our findings illustrate that although the percentage of protein in the food of juvenile lobsters may be similar, the use of the nitrogen component is significantly different. We conclude that the quality of the protein in a diet may be as important (if not more important) as its quantity.

Le taux d'excrétion de déchets azotés est fonction non seulement du métabolisme d'un animal mais aussi de la valeur nutritionnelle et de la quantité de protéines entrant dans le régime alimentaire. On a mesuré pendant 24 h après l'alimentation le taux horaire d'excrétion d'ammoniac chez de jeunes homards, *Homarus americanus*, appartenant aux stades V et VI qu'on a nourri d'aliments purifiés préparés à partir de la caséine ou d'une protéine purifiée de crabe, pour déterminer les différences dans l'efficacité d'utilisation de ces deux protéines. Les taux horaires d'excrétion d'ammoniac par les homards des stades V et VI nourris d'aliments à base de caséine ont été beaucoup plus élevés que ceux des animaux nourris d'aliments à base de protéine de crabe. En plus des différences dans le taux d'excrétion d'ammoniac observées entre les animaux qui ont été soumis aux deux régimes, on a noté entre les homards des stades V et VI soumis à chaque régime des variations périodiques régulières mais différentes du taux horaire d'excrétion. Nos résultats montrent que, même si le pourcentage de protéines dans la nourriture des jeunes homards est semblable, l'utilisation de l'élément azote est très différente. Nous concluons que la qualité de la protéine dans un régime alimentaire est aussi importante (sinon plus) que la quantité fournie.

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Many studies have examined nutrition in the American lobster, *Homarus americanus* (Conklin 1980; McVey 1983). Most of these studies have been directed towards evaluating natural and artificially formulated diets for their use in aquaculture. Vitamin-free casein, a milk protein, has been widely used as an artificial protein source. Certain essential amino acids are limiting, however, and are required in elevated concentrations in formulated diets (Mason and Castell 1980). Boghen et al. (1982) and J. D. Castell (unpubl. data) found that a protein purified from the rock crab *Cancer irroratus*, resulted in growth and survival of juvenile lobsters when it was used to replace casein in purified test diets.

Further investigations of crab protein indicated higher growth potential and survivorship in lobsters over a diet based on casein as the major protein source (J. D. Castell, unpubl.

[1] This work was completed in partial fulfillment of the requirements for the degree of Bachelor of Science at Dalhousie University, Halifax, N.S.

TABLE 1. Composition of experimental diets fed to test lobsters expressed on a percent dry weight basis.

Ingredient	Composition (% dry weight)
Major	
Diet 1: casein	50
Diet 2: crab (purified *Cancer irroratus* protein)	50
Minor (both diets)	
Gelatin	10
α-Cellulose	10.8
Cornstarch	5
Mineral supplement	5
Cholesterol	1
Cod liver oil	9
Vitamin supplement	1
Soya licithin	6
DL-α-Tocopherol	0.2
Choline chloride	1

data). To investigate whether metabolism of nitrogen is the key factor causing the crab diet to be superior to the casein diet, we compared use efficiencies of the two nitrogen sources by juvenile American lobsters. We hypothesized that under similar test conditions animals would show different rates of ammonia excretion (i.e. nitrogen catabolization) depending on the quality more than the quantity of the protein source supplied. Consequently, the higher the ammonia excretion per unit time the less nitrogen would be available for incorporation into anabolic processes and vise versa.

In addition to evaluating nitrogen use, we also investigated fluctuations in ammonia excretion by juvenile lobsters. Results from other researchers studying marine Crustacea indicate a wide variation in patterns and rates of ammonia release (Kirby and Harbaugh 1974; Gardner and Scavia 1981; Gardner and Paffenhöfer 1982; and others). However, most of these studies were not carried out over a 24-h cycle.

Materials and Methods

Freshly hatched larvae from a single wild-stock American lobster were raised according to Castell (1977). Individuals were randomly placed in Plexiglas trays in laboratory rearing tanks with continuous flowing seawater at 20 ± 0.5°C and 32‰ salinity. Stages V and VI animals fed the crab diet weighed 59.4 ± 6.9 mg wet weight (n = 7) and 82.0 ± 18.5 mg wet weight (n = 14), respectively, with those fed the casein diet weighing 60.5 ± 6.7 (n = 6) and 86.3 ± 18.2 mg wet weight, respectively. Two rearing conditions were established, one with individuals fed a casein-based diet (Mason and Castell 1980) and the other with individuals fed a purified crab protein-based diet (J. D. Castell, unpubl. data). Lobsters were exposed to their respective diets for a period of 5 wk and were fed ad libatum three times per day. At each feeding time excess uneaten food and fecal material were removed before fresh food was presented. Final feeding occurred 2 h prior to excretion experiments. Photoperiod was held at a 12 h light : 12 h dark cycle during rearing and experimentation.

The composition of the two experimental diets is shown in Table 1. Each diet is identical except for the source of the protein component, which comprised 50% of the diet on a dry weight basis.

Juvenile lobsters were tested over a period of 24 h in an attempt to determine whether there was any diurnal rythmic or irregular pattern in the excretion of ammonia.

For ammonia excretion measurements, single individuals were transferred to L-shaped Plexiglas vials filled with 5 mL of 0.5-μm-filtered, oxygen-saturated seawater at 20 ± 0.5°C and salinity of 32‰. Chemical analysis for ammonia nitrogen followed the automated method of Hawkins and Keizer (1982), with each vial sampled at about 0.8-h intervals over a period of approximately 24 h. Water in sample and control vials was renewed with fresh oxygen-saturated and ammonia-free seawater at approximately 4-h intervals throughout the experiment to prevent undue stress associated with lowering oxygen concentrations in the sample vials (Kirby and Harbaugh 1974). In addition, any visible evidence of fecal material was removed at this time. At the termination of the experiment, each individual was blotted dry to remove excess water and its fresh weight recorded to the nearest milligram.

Rates of ammonia excretion were expressed as μg-at $N \cdot g$ wet weight$^{-1} \cdot h^{-1}$. Changes in sample volume were considered in calculating hourly rates of excretion.

Mean (±SE) hourly rates of ammonia excretion were determined for lobsters exposed to two test diets. Hourly excretion rates measured over the entire sampling period were then pooled for individuals exposed to each diet and the resulting means subjected to paired t-tests to assess significance.

Results

Mean hourly rates of ammonia nitrogen excretion measured over approximately 26 h for Stage V lobsters fed the casein-based protein diet (n = 6 individuals) and the crab protein-based diet (n = 7 individuals) are shown in Fig. 1. When hourly values for ammonia excretion were pooled over the entire sampling period, and an overall mean calculated, Stage V lobsters fed the casein-based protein diet excreted significantly more nitrogen in the form of ammonia ($P < 0.01$) than their cohorts fed the crab-based protein diet. Mean hourly rates of ammonia excretion by Stage VI lobsters fed the crab-based protein diet (n = 14) and casein-based protein diet (n = 12) examined over approximately 24 h are shown in Fig. 2. Unfortunately, instrument failure during the initial 4 h of the experiment prevented recording of data. When all hourly rates of ammonia excretion were pooled over the complete sampling period, the mean hourly rate of ammonia excretion for casein-fed animals was significantly higher ($P < 0.01$) than the mean hourly rate of ammonia excretion by cohorts fed the crab diet.

Inspection of both figures indicates a regular, rhythmic pattern to ammonia excretion in Stages V and VI lobsters fed each diet. In Fig. 1, peaks and troughs of ammonia excretion occur at about 6-h intervals for Stage V lobsters fed each diet. A similar pattern is shown in Fig. 2 where peaks and troughs occur at approximately 4-h intervals for Stage VI lobsters fed each diet. In addition, the pattern of ammonia excretion does not appear to be affected by the photoperiod. In both Stage V and Stage VI individuals there is consistency to the rhythm of ammonia excretion throughout the day and night conditions. The pattern of excretion is not disrupted at the onset of night or day nor during total light or darkness.

The renewal of the media does not appear to significantly affect the pattern of ammonia excretion (Fig. 1 and 2). In Stage V lobsters fed each diet, a pattern established several samplings before the renewal of the media was still followed after the renewal had taken place. This continuing of an established trend also occurred in the Stage VI lobsters fed each diet. We

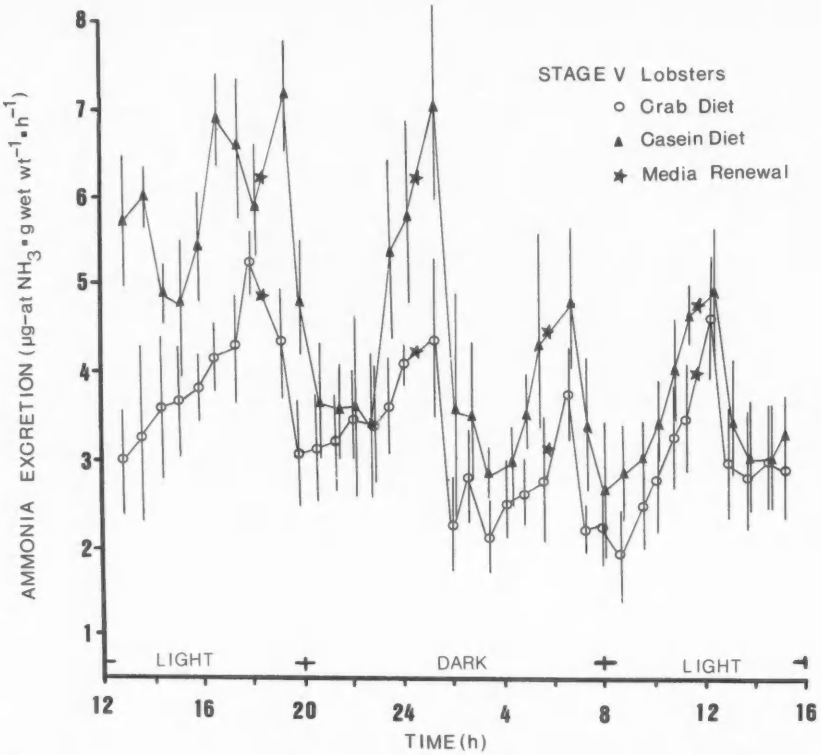

FIG. 1. Hourly rates of ammonia excretion by Stage V lobsters fed either casein- (n = 6) or crab-based (n = 7) protein diets. Solid lines that connect the data points are for convenience in interpretation.

believe that the strong consistency in the data indicates no marked affect of the renewal procedures on the excretion rate in any of the tests conducted.

Discussion

The retention of nitrogen for the use in anabolic processes is essential for growing animals. Thus, it would be an advantage for individuals to conserve nitrogen and minimize the excretion of nitrogenous waste products. However, the nature of the protein component of a diet (i.e. the major nitrogen carrier) may reduce this advantage. Consequently, diets whether artificial or natural which have particulate nitrogen in a less or more available form will prove inferior or superior for use in anabolic processes. Acquaculturists should consider this is to maximize growth over the shortest period of time. The present study, in conjunction with previous work showing better growth with crab protein (J. D. Castell, unpubl. data), illustrates that the crab protein-based diet is clearly a more superior diet than the casein-based protein diet, as the excretion of nitrogen in the form of ammonia is significantly less in both stages of the lobsters examined.

Although the digestibility of amino acids may be a limiting factor in the metabolism of protein, it was not examined in the present study. Casein supplemented with various concentrations of amino acids has been shown by Mason (1977) to increase growth in juvenile lobsters, but similar studies have not been undertaken with crab protein. Studies of amino acid digestibility in juvenile lobsters fed both a casein and crab protein base diet are needed to further delineate the causative factors resulting in differences in nitrogen excretion attributed to the metabolism of diets which differ in their source of protein.

Other researchers have measured the excretion of ammonia by lobsters fed a natural protein-based diet. Logan and Epifanio (1978) measured the average hourly rate of ammonia excretion of Stages I–XI lobsters fed brine shrimp. From their data we calculated hourly excretion rates of 3.9 and 3.5 µg-at N·g wet weight^{-1} for Stage V and Stage VI lobsters, respectively. In the present study the ammonia excretion rate over the complete sampling period ranged between 1.88 and 4.95 µg-at N·g wet weight^{-1}·h^{-1} for Stage V lobsters fed the crab diet and between 2.66 and 7.20 µg-at N·g wet weight^{-1}·h^{-1} for individuals fed the casein diet. Pooled data over the complete sampling period yielded a mean (±95% C.L.) excretion rate of 4.38 ± 0.23 µg-at N·g wet weight^{-1}·h^{-1} for animals fed the casein diet and 3.25 ± 0.12 µg-at N·g wet weight^{-1}·h^{-1} for animals fed the crab diet. This latter value compares well with that value calculated from the data of Logan and Epifanio (1978). Similarly, for Stage VI lobsters examined in the present study, values of ammonia excretion rate for animals fed the crab diet ranged between 1.51 and 4.24 µg-at N·g wet weight^{-1}·h^{-1} as compared with 1.82 and 5.65 µg-at N·g wet weight^{-1}·h^{-1} for animals fed the casein-based diet. The mean (±95% C.L.) excretion rate over the entire sampling period for Stage VI lobsters fed the casein diet was 3.44 ± 0.21 µg-at N·g wet weight^{-1}·h^{-1} compared with 2.87 ± 0.12 µg-at N·g wet weight^{-1}·h^{-1} for cohorts fed the crab diet. The mean hourly

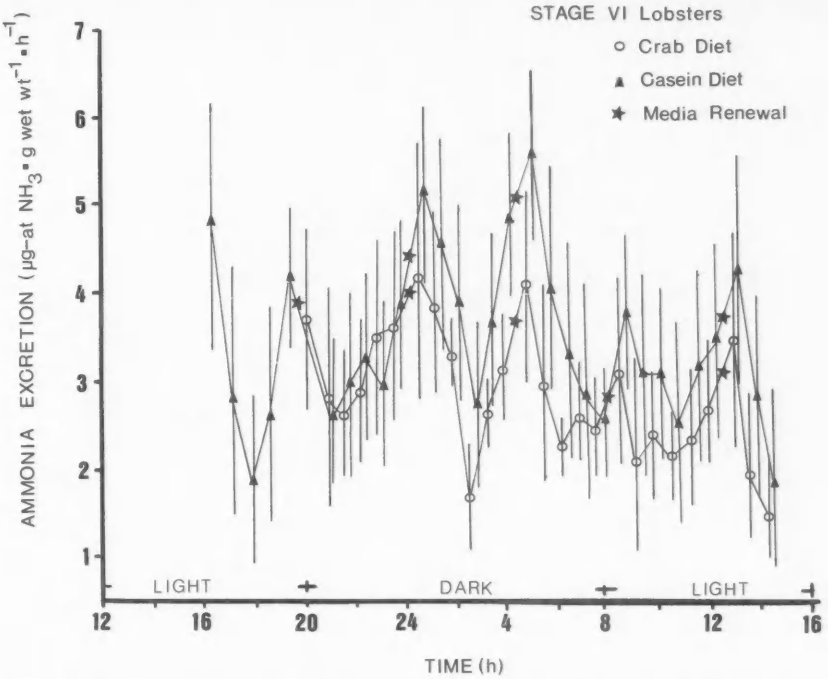

FIG. 2. Hourly rates of ammonia excretion by Stage VI lobsters fed either casein- (n = 12) or crab-based (n = 14) protein diets. Solid lines that connect the data points are for convenience in interpretation.

excretion rate for Stage VI animals fed the crab diet was slightly but not significantly lower than the average value calculated from the data of Logan and Epifanio (1978) (2.78 versus 3.46 µg-at N·g wet weight^{-1}·h^{-1}).

Logan and Epifanio (1978) have further calculated the minimum percentage of protein required by juvenile lobsters with the assumed values of 6.25 g protein·g N^{-1} and 3 Kcal·g food^{-1}. Their minimum estimate for protein content in food to maintain juvenile lobsters was 17.4%. However, they recognized that the actual value is likely to be higher to account for nitrogenous waste products other than ammonia and the loss of nitrogen as glucosamine (chitin) at each molt. A higher percentage of protein in the diet is thus necessary for growth. Our results, which show that the two diets of equal protein level (50% by dry weight) are not used with the same efficiency, indicate that the quality of the protein source in a diet is a significant factor in the nutrition of juvenile lobsters. Consequently, formulated or natural diets selected to improve growth in commercial species should be tested for nitrogen use and not be solely based on a high protein level. The quality of the protein in terms of the use of its nitrogen component may be the key factor in assessing growth rather than high levels of relatively refractory protein.

Our study showed two additional important features with respect to nitrogen metabolism in juvenile lobsters. First, rates of ammonia excretion were not significantly affected by the photoperiod. Both figures indicate that excretion rates did not change in their established pattern over the 24 h. Second, there is a marked rhythmic pattern of ammonia excretion. Patterns of ammonia excretion have been examined in many Crustacea, but most of these studies have been conducted on groups of individuals incubated in sealed vessels for long periods of time (4+ h) or studies on single individuals incubated over short periods of time (see Hawkins and Keizer 1982 for discussion). Our study illustrates that a rhythmic pattern of ammonia excretion occurs in both states of the lobsters examined and with each diet. In Stage V animals, peaks in ammonia excretion occur at approximately 6-h intervals, while in the Stage VI animals the period is reduced to approximately 4 h. The cause of the rhythmic pattern of ammonia excretion may be related to endogenous cycles influencing physical activity, digestive processes, hormonal secretions, or their combinations.

Adult *H. americanus* exhibited a peak in physical activity before dark, correlated with the departure from a den and probable subsequent increase in social activity (Phillips et al. 1980). We recorded a peak in ammonia excretion by both stages fed either diet prior to darkness. We also recorded a peak in nitrogen release before light conditions. By extending the speculation of Phillips et al. (1980), this latter peak in ammonia excretion may be related to an increase in activity associated with searching for dens as dawn approaches.

We revealed other peaks in ammonia release at regular intervals. These observations may reflect the influence of digestive and hormonal processes acting over and above the influence on ammonia excretion caused by physical activity. Hormones are apparently involved in the control of ammonia excretion in the prawn *Macrobrachium lanchesteri* (Raman et al. 1981); and digestive enzyme secretion varies considerably with time after feeding in the European lobster *Homarus gammarus* (Barker and Gibson 1977). Although we are unaware of the patterns and rates of hormonal and enzyme secretory activity in juvenile *H. americanus*, interactions may occur which influence the

periodicity of excretion we observed.

In summary, the excretion experiments with Stages V and VI cohorts of the American lobster fed diets differing in protein source illustrate that although the percentage of protein in the food may be similar, the use of the nitrogen component may be significantly different. Thus the quality of the protein in a diet may be as important (if not more important) as its quantity. In addition, the time series observations on individuals incubated over a 24-h period indicate that ammonia excretion is not markedly influenced by photoperiod but shows a regular recurring pattern. To our knowledge, this pattern of ammonia excretion has not been shown in other decapod Crustacea.

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References

BARKER, P. L., AND R. GIBSON. 1977. Observations on the feeding mechanism, structure of the gut, and digestive physiology of the European lobster *Homarus gammarus* (L.) (Decapoda:Nephropidae). J. Exp. Mar. Biol. Ecol. 26: 297–324.

BOGHEN, A. D., J. D. CASTELL, AND D. E. CONKLIN. 1982. In search of a reference protein to replace "vitamin-free casein" in lobster nutrition studies. Can. J. Zool. 60: 2033–2038.

CASTELL, J. D. 1977. Production of juvenile lobsters (*Homarus americanus*) for nutrition research. Actes Colloq. CNEXO 4: 277–281.

CONKLIN, D. E. 1980. Nutrition, p. 277–300. *In* J. S. Cobb and B. F. Phillips [ed.] The biology and management of lobsters. Vol. I. Academic Press, New York, NY.

GARDNER, W. S., AND G. A. PAFFENHÖFER. 1982. Nitrogen regeneration by the subtropical marine copepod *Eucalanus pileatus*. J. Plant Res. 4(3): 725–734.

GARDNER, W. S., AND D. SCAVIA. 1981. Kinetic examination of nitrogen release by zooplankters. Limnol. Oceanogr. 26(5): 801–810.

HAWKINS, C. M., AND P. D. KEIZER. 1982. Ammonia excretion in *Corophium volutator* using an automated method. Can. J. Fish. Aquat. Sci. 39: 640–643.

KIRBY, P. K., AND R. D. HARBAUGH. 1974. Diurnal patterns of ammonia release in marine and terrestrial isopods. Comp. Biochem. Physiol. 47(A): 1313–1321.

LOGAN, S. T., AND C. E. EPIFANIO. 1978. A laboratory energy balance for the larvae and juveniles of the American lobster *Homarus americanus*. Mar. Biol. 47: 381–389.

MASON, E. G. 1977. Dietary amino acid requirements of juvenile lobsters (*Homarus americanus*). M.Sc. thesis, Dalhousie University, Halifax, N.S. 151 p.

MASON, E. G., AND J. D. CASTELL. 1980. The effect of supplementing purified proteins with limiting essential amino acids on growth and survival of juvenile lobsters (*Homarus americanus*). Proc. World Maricult. Soc. 11: 346–354.

MCVEY, J. P. 1983. Handbook of mariculture. Vol. 1. Crustacean aquaculture. Section IV: Crustacean nutrition, p. 381–423. CRC Press Inc., Boca Raton, FL.

PHILLIPS, B. F., J. S. COBB, AND R. W. GEORGE. 1980. Chapter 1. General biology, p. 2–72. *In* J. S. Cobb and B. F. Phillips [ed.] The biology and management of lobsters. Academic Press, New York, NY. 463 p.

RAMAN, K. V. A., K. SHAKUNTALA, AND R. REDDY. 1981. Influence of endogenous factors on the pattern of ammonia excretion in the prawn *Macrobrachium lanchesteri* (de Man). Indian J. Exp. Biol. 19: 42–45.

Estimating Fork Lengths of Fathead Minnows, *Pimephales promelas*, from Measurement of Pharyngeal Arches

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McIntyre, D. B., and F. J. Ward. 1986. Estimating fork lengths of fathead minnows, *Pimephales promelas*, from measurement of pharyngeal arches. Can. J. Fish. Aquat. Sci. 43: 1294–1297.

The pharyngeal arches of fathead minnows (*Pimephales promelas*) are persistent in the gut of juvenile walleye (*Stizostedion vitreum vitreum*). The relationship of fork length to GAP (chord length between the dorsal and ventral extremities of the left pharyngeal arch) measurements of left pharyngeal arches of fathead minnows is linear, positive, and highly significant. Fish lengths calculated from arches recovered from stomachs after a period of up to 8 h generally fell within the prediction intervals established for the regression of fork lengths on arch measurements of freshly killed minnows. The relationship between length and arch measurement will permit the length of ingested fathead minnows to be calculated aiding in food size selection and energetic studies. Other minnow species, sharing the same habitats with fathead minnows, have distinctive pharyngeal arches which can be used to identify species in stomach contents. Length may also be correlated with pharyngeal arch measurements in these species.

Les arcs pharyngiens des têtes-de-boule (*Pimephales promelas*) persistent dans le système digestif des jeunes dorés jaunes (*Stizostedion vitreum vitreum*). La relation de la longueur à la fourche par rapport aux mesures GAP (longueur de la chorde entre les extrémités dorsale et ventrale de l'arc pharyngien gauche) d'arcs pharyngiens gauches de têtes-de-boule est linéaire, positive et très significative. La longueur des poissons calculée à partir des arcs retrouvés dans les estomacs après une période pouvant aller jusqu'à 8 h tombait généralement à l'intérieur

des intervalles de prédiction établis pour la régression des longueurs à la fourche par rapport aux mesures des arcs de ménés fraîchement tués. La relation entre la longueur et la mesure de l'arc va permettre de calculer la longueur des têtes-de-boule ingérés facilitant la sélection de la taille des particules de nourriture et les études énergétiques. D'autres espèces de ménés, partageant avec les têtes-de-boule le même habitat, ont des arcs pharyngiens distincts dont on peut se servir pour identifier les espèces présentes dans les contenus stomacaux. La longueur peut également être mise en corrélation avec les mesures des arcs pharyngiens chez ces espèces.

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Determination of the size of food items is important in evaluating size selectivity, i.e. comparisons between sizes of animals available in the environment in contrast with sizes ingested. Another application is in energetics. Accurate estimates of the energy content of partially digested remains may be difficult to determine, but if the size at ingestion can be estimated, more precise calorific values can be obtained.

Sizes of forage fish ingested by vertebrate predators can sometimes be estimated from stomach contents (Bradstreet 1980). Sections of vertebral columns (Pikhu and Pikhu 1970) and opercular bones (Newsome 1977) have been used to estimate sizes of several species ingested by predatory fishes. Weights of some cyprinids and catostomids were related to measurements of their pharyngeal arches (Casteel 1972).

In field and laboratory studies, we have used the fathead minnow, *Pimephales promelas*, as a food for juvenile walleye, *Stizostedion vitreum vitreum*. Until recently we have not been able to estimate the lengths of partly digested fathead minnows because soft parts are soon destroyed; however, the pharyngeal arches are persistent. They can be identified in the intestine as well as in the stomach. Furthermore, they are seldom fragmented although left and right arches may be separated.

Our purpose is to describe a procedure using the relationship between a measurement of the pharyngeal arch and known length of fish to predict lengths of fathead minnows. We also investigated the effects of residence time in walleye stomachs on the precision of estimates.

Methods

Pharyngeal arches were removed and fork lengths measured from fresh fish captured in June and July 1985. Fork lengths were measured to the nearest 0.5 mm.

Each of four length groups of fathead minnows (25, 33, 43, and 53 mm) was placed in a 40-L aquarium containing juvenile walleye (fork lengths 76−215 mm) which had been starved for 24 h. After 5 h at 20°C, the walleyes were killed and any partly digested fathead minnows were removed from their stomachs. In a second experiment, walleye were retained for 8 h at 20°C after the minnows were introduced.

Steps in removing the left pharyngeal arches from fathead minnows were as follows: (1) remove the left operculum; (2) remove the gill arches exposing the pharyngeal arch, located ventral and slightly anterior to the cleithrum; (3) using fine tipped forceps, grip the left pharyngeal arch and, with moderate traction, withdraw the arch; (4) with forceps remove muscle tissue adhering to the arch. The degree of difficulty in removing pharyngeal arches from ingested minnows ranged from the procedure described above to removing them from partially digested tissue.

A dissecting microscope with a calibrated eyepiece was used to determine the length of a chord measured between the dorsal and ventral extremities of the left pharyngeal arch (Fig. 1). This measurement is named the GAP.

Relationships between length and GAP were determined using a simple regression analysis (Helwig and Council 1979).

Results

The relationship of fork length to GAP of freshly caught fathead minnows is linear (Fig. 2) and highly significant ($r^2 = 0.974$; $F = 3244$; df = 88; $P < 0.01$). The equation for the line is FL = 13.481GAP + 1.963.

Confidence intervals for five selected adjusted fork lengths are narrow (Table 1). Using the equation, the confidence interval about the line should be within ±4% for small fatheads, about 18 mm, and ±2% for larger fish, about 60 mm.

A total of 19 partly digested minnows from 25 to 53 mm long (lengths determined prior to introduction to the aquaria containing walleye) were recovered from walleye at the end of the 5-h feeding experiment. Eighteen fathead minnows from 25 to 43 mm long were recovered from walleye held with minnows for 8 h.

Fork lengths predicted from pharyngeal arches recovered from partially digested minnows generally fell within the prediction intervals (PI). For example, PI's were ±14.6 and 6.4% for predicted fork lengths of 25.7 and 52.8 mm, respectively. No estimated length fell outside the appropriate PI determined from arches recovered from walleye held for 5 h and only one from the 8-h experiment. In this case the predicted fork length was 4.5 mm less than the actual length whereas the interval was ±3.8 mm.

Discussion

The highly significant *F*-value and the narrow confidence interval band about the regression of fork lengths on GAP indicated that the relationship is a very close one, considerably improved over that obtained for fathead minnow lengths estimated from opercular bone measurements (Newsome 1977). Neither confidence intervals nor prediction intervals were presented for the vertebral column method (Pikhu and Pikhu 1970). Casteel (1972), studying native Californian catostomids and cyprinids, transformed both pharyngeal arch measurements and weights to calculate linear regressions; therefore, his method is not directly comparable with ours and his study did not include the fathead minnow.

Popova (1967) reported that Kovalev, in a 1958 paper, determined body sizes from measurements of the suprapharyngeal bones of certain fish from the Volga delta. We have not been

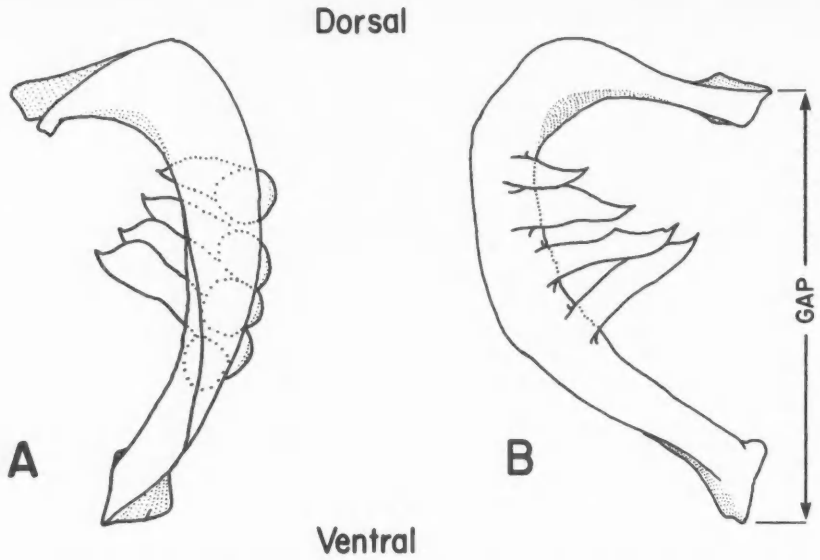

FIG. 1. (A) Anterior and (B) posterior views of the left pharyngeal arch of a fathead minnow showing the GAP measurement.

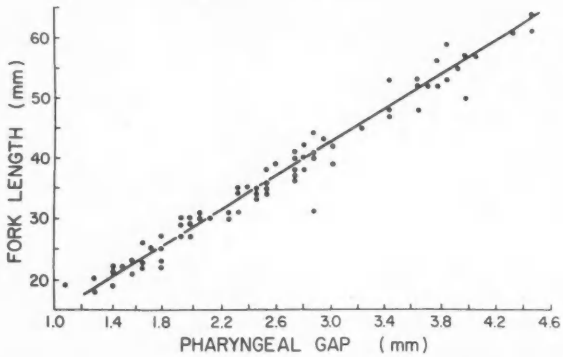

FIG. 2. Relation between fork length and pharyngeal GAP of freshly killed fathead minnows.

TABLE 1. Confidence intervals (95%) for the regression of fork lengths (mm) on GAP measurements (mm) for fathead minnows.

GAP	Adjusted fork length	CI	Percent
1.2	18.146	±0.742	4.1
2.4	34.324	±0.395	1.2
2.8	39.716	±0.410	1.0
4.8	66.678	±1.136	1.7
5.2	72.070	±1.314	1.8

able to locate a copy of this paper.

Digestion of stomach contents of walleye sacrificed after 8 h was more advanced than in fish sacrificed after 5 h, but relatively undigested minnows were present in walleye stomachs from both experimental groups. Variability in degree of digestion was related to the size, number consumed (Swenson and Smith 1973), and, probably, the residence time of minnows in the gut. However, GAP measurement was not seriously affected by gut residence times of up to 8 h; therefore, degree of digestion does not seriously reduce the accuracy of the method.

Our method may be limited to cyprinids, although it probably could be applied to catostomids (Casteel 1972). We have measured pharyngeal arches and fork lengths of small samples of preserved emerald shiners (*Notropis atherinoides*) and spottail shiners (*Notropis hudsonius*) and have observed a strong positive and linear relationship between arch measurements and fork lengths in both. We have also noted clear differences in size and shape of the arches exclusive of differences in pharyngeal tooth number and pattern (Scott and Crossman 1973). Minnow remains in stomachs can usually be identified by these means. Perhaps the size distributions of each species ingested could also be estimated.

Acknowledgments

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References

BRADSTREET, M. S. W. 1980. Thick-billed murres and black guillemots in the Barrow Strait area, N.W.T., during spring: diets and food availability along ice edges. Can. J. Zool. 58: 2120–2140.

CASTEEL, R. W. 1972. The use of fish remains in archeology with special reference to the native freshwater and anadromous fishes of California. Ph.D. thesis, University of California, Davis, CA. 751 p.

HELWIG, J. T., AND K. A. COUNCIL. 1979. SAS user's guide. 1979 ed. SAS Institute Inc., Cary, NC. 494 p.

NEWSOME, G. E. 1977. Use of opercular bones to identify and estimate lengths

of prey consumed by piscivores. Can. J. Zool. 55: 733–736.

PIKHU, E. KH., AND E. R. PIKHU. 1970. Reconstruction of the sizes of fishes swallowed by predators from fragments of their vertebral column. J. Ichthyol. (U.S.S.R.) 10: 706–709.

POPOVA, O. A. 1967. The 'predator–prey' relationship among fishes (a survey of Soviet papers), p. 359–376. *In* S. D. Gerking [ed.] The biological basis of freshwater fish production. Blackwell, Oxford and Edinburgh.

SCOTT, W. B., AND E. J. CROSSMAN. 1973. Freshwater fishes of Canada. Bull. Fish. Res. Board Can. 184: 966 p.

SWENSON, W. A., AND L. L. SMITH JR. 1973. Gastric digestion, food consumption, feeding periodicity, and food conversion efficiency in walleye (*Stizostedion vitreum vitreum*). J. Fish. Res. Board Can. 30: 1327–1336.

PERSPECTIVES

Decline in Natural Fisheries — A Genetic Analysis and Suggestion for Recovery

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Overfishing and pollution of the aquatic environment, in addition to their direct effects on natural fisheries, may have also influenced natural fish populations genetically. Overfishing drastically reduces population size and, since the larger individuals are selectively removed, is equivalent to selection for smaller sized fish. Adaptation of natural fish populations to their environment must have been reduced by rapid environmental changes resulting from pollution and infestation. Inbreeding, negative selection, and lack of adaption are here considered as the genetic causes for the decline of natural fisheries and lack of recovery. Restocking programs involving hatchery stocks are unlikely to solve this problem, since these stocks were selected for adaptation to hatchery environments and not to natural environments. A series of studies have demonstrated heterosis of interstrain crossbreds, mainly between hatchery and wild stocks of salmonids, for performance in natural waters. Two strategies could be implemented in restocking programs: stocking spawners of a domestic strain (preferably of one sex) for interbreeding with the resident population or direct stocking of crossbred fry. This should be tested in small isolated bodies of water and needs to be accompanied by a monitoring program in order to evaluate the results and minimize hazards.

En plus de leurs effets directs sur les pêches, la surpêche et la pollution naturelles de poisson. La surpêche se traduit par une réduction très marquée de la taille des populations et, comme les individus les plus gros sont sélectivement capturés, elle équivaut à une sélection en faveur des poissons de plus petite taille. L'adaptation des popultaions naturelles de poisson à leur milieu doit avoir été réduite par les modifications rapides de d'environnement causées par la pollution et les infestations. L'auteur considère la consanguinité, la sélection négative et le manque d'adaptation commel es causes génétiques du déclin des populations naturelles exploitées et de l'absence de leur rétablissement. Il est peu probable que les programmes de rétablissement des stocks faisant appel à la pisciculture permettent de résoudre ce problème car la sélection de ces stocks est fonction de leur adaptabilité au milieu piscicole et non au milieu naturel. Plusieurs études ont montré que l'hétérosis obtenue suite au croisement entre souches, surtout entre stocks piscicoles et sauvages de salmonidés, favorisait le rendement en eaux naturelles. Deux stratégies de repeuplement pourraient être mises en œuvre : le repeuplement par une souche piscicole (de préférence des individus de même sexe) pour croisement avec la population indigène, ou le repeuplement direct par alevins obtenus par croisement. Ces essais devraient être réalisés dans de petits plans d'eau isolés et être contrôlés de façon à évaluer les résultats et à minimiser les risques.

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A serious decline in many commercial and sports fisheries has occurred during the present century, which in some cases has led to a complete collapse. This decline has been documented for some lakes and rivers, particularly the Great Lakes of North America (e.g. Berst and Spangler 1972; Christie 1972; Lawrie and Rahrer 1972; Loftus 1976; Kenyon 1978). Similar declines have occurred, or are occurring, in other freshwater fisheries as well as in the oceans. The primary causes of these declines are likely to be due to an intensification of fishing resulting in overexploitation, and changes in the aquatic environment, such as pollution, infestation, and topographical alterations in shore lines. These factors must have resulted in genetic changes in the fish populations involved and reduced their adaptation to the changed environments. Fishery management aimed at restoring collapsed fisheries, or at least preventing further declines, generally consists of limitation of fishing pressure, improvement of water quality, control of infestations, and restocking programs. The possibility that genetic changes have occurred in fish populations is generally not taken into account (Handford et al.

1977) due to a lack of understanding of fish genetics (Larkin 1979). The objectives of this paper are to (1) point out the possible genetic implications of overexploitation and pollution, (2) show that presently practiced restocking programs may involve unsuitable fish genotypes, (3) suggest the use of crossbreds between strains by summarizing and synthesizing the results of a number of studies in which interstrain crossbreds of different salmonids were compared with their parental strains, and (4) indicate a research program for testing this system.

Genetic Effects of Overexploitation

In very heavily exploited populations, the number of survivors may become so low as to bring about an inbreeding effect, since the coefficient of inbreeding is an inverse function of the effective number of parents (Falconer 1960). This may result in inbreeding depression, causing a reduction in traits such as survival, fertility, growth rate, disease resistance, etc. A single disastrous season, in which the number of spawners (of at least one sex) is reduced drastically, may bring about a long-term inbreeding effect. In addition, the individuals removed by fishing are not a random sample of the multispecies population, but rather the larger and more catchable ones. Removing the larger individuals from a population is equivalent to selecting the smaller ones as parents for the next generation. The long-term effects of this negative selection depend on the intensity of fishing and the phenotypic variation and heritability of growth. Under these circumstances a decrease in growth may result even at low heritabilities.

Lack of Adaptation to Rapid Environmental Changes

The adaptation of a natural population to its environment is a result of the action of natural selection. This mechanism brings about adaptive changes in allelic frequencies in response to *gradual* changes in the environment. However, changes in aquatic environmental conditions (e.g. pollution or faunistic changes such as the invasion of the upper Great Lakes of North America by the sea lamprey (*Petromyzon marinus*) (e.g. Berst and Spangler 1972; Wells and McLain 1972)) have occurred mainly in the present century, too rapidly for the action of natural selection, which is a slow process. Therefore, natural populations in polluted or infested waters are unlikely to have adapted to these new environments and are expected to decline as a result.

Results of Negative Selection and Lack of Adaptation on Wild Fish Populations

When the single causative agency is the direct effect of overfishing, the immediate result is a decrease in the number of fish, thence a decrease in absolute catch or catch per unit effort. This is expected to be accompanied by an increase in size of fish, resulting from a larger amount of food organisms being available per individual (Colby et al. 1972). An initial increase in size of fish in overexploited populations has been shown for walleye (*Stizostedion vitreum vitreum*) in Lake Nipissing, Ontario (Anthony and Jorgensen 1977), and yellow perch (*Perca flavescens*) in Lake Huron (Eshenroder 1977). However, eventually fish size often decreases as a result of overexploitation in spite of their reduced number, e.g. the larger deepwater ciscoes (*Coregonus nigripinnis* and *C. johannae*) in Lake Michigan (Wells and McLain 1972), lake whitefish (*Coregonus clupeaformis*) in Lakes Winnipeg and Erie (Davidoff et al. 1973; Kenyon 1978), lake whitefish and lake trout (*Salvelinus namaycush*) in Great Slave Lake (Canadian Northwest Territories) (Keleher 1972), coho, chinook, and pink salmon (*Oncorhynchus kisutch, O. tshawytscha, O. gorbuscha*) in British Columbia (Ricker 1981), and Nile tilapia (*Tilapia nilotica*) in Lake George, Uganda (Gwahabe 1973). This decreased size, in spite of greater food availability, is most reasonably explained by negative genetic changes in the fish resulting from the negative selection accompanying overfishing. Indirect effects of pollution, lack of adaptation to the polluted environment, include an "increased vulnerability to changes in other stresses such as fishing" (Colby et al. 1972). I have not found any historical documentation of a fishery which was polluted but not overfished. In the Lesser Slave Lake (central Alberta), populations of whitefish and ciscoes were exposed to both overexploitation and pollution. By the time this fishery collapsed the mean weight of fish was less than half of what it had been 30 yr previously (Handford et al. 1977). This may be a combined result of pollution, a lack of genetic adaptation to this polluted environment as well as the negative effect of overfishing. Changes in populations resulting from the effects of pollution are more clearly seen by comparing catch compositions between rather than within species. With progressively increasing pollution, a succession in relative abundance occurs from species less adapted to those more adapted to polluted conditions (Colby et al. 1972; Laurent 1972; Roth and Geiger 1972).

Development of Domestic Strains

Stocking hatchery-raised fish has long been a method of attempting to improve or restore commercial or sports fisheries in lakes and rivers. Hatchery personnel, producing these fish, soon became aware of the difficulties of handling wild strains in a hatchery and rearing their fry. These difficulties are due to the lack of adaptation of wild strains to artificial environments, making wild strains of rainbow trout (*Salmo gairdneri*), for example, unsuitable for hatchery operations (Cordone and Nicola 1970).

In response to these difficulties in manipulating wild strains of fish in hatcheries, domestic strains were developed at different research institutes and hatcheries for adaptation to hatchery conditions, without testing their performance in the wild. The domestic strains developed differ from wild strains in traits such as growth rate in the hatchery, earlier maturity, tolerance to higher temperatures, egg production, resistance to hatchery diseases, etc. (Embody and Hayford 1925; Hayford and Embody 1930; Lewis 1944; Donaldson and Menasveta 1961; Toney and Bowen 1968; Bruhn and Bowen 1973). This process resulted in reducing the cost of producing a unit weight of trout from domestic strains to between one third and one sixth of that when wild strains are used (Smith 1961; Cordone and Nicola 1970; Rawstron 1972, 1973). But when stocked into streams or lakes, domestic strains were found to be inferior to wild strains in survival, growth, and quality (Millenbach 1950; Miller 1952, 1958; Smith 1961; Flick and Webster 1964). This may be a result of a (negative) correlated response for performance in the wild, which was ignored in the hatchery selection programs.

Use of Crossbreds between Different Strains

It is apparent that neither wild nor domestic strains are satisfactory for stocking into natural waters. A possible solution to

TABLE 1. Performance of domestic, wild, and domestic × wild strain cutthroat trout stocked into Echo Lake, Washington, in 1954 (after Donaldson et al. 1957). Domestic = a strain of cutthroat trout selected at University of Washington for 20 yr; wild = first generation progeny of cutthroat trout taken from Lake Whatcom, Washington.

Stock	Weight per fish (g)			Percent caught of no. planted		Percent catch of weight planted	
	Initial	1-yr-olds	2-yr-olds	1-yr-olds	2-yr-olds	1-yr-olds	2-yr-olds
Domestic (♀) × domestic (♂)	5.18	98.4	289.3	0.99	0.30	19.0	16.7
Domestic (♀) × wild (♂)	5.46	79.2	256.0	5.60	0.85	89.6	40.3
Wild (♀) × domestic (♂)	5.18	88.5	338.3	6.20	0.44	106.3	28.6
Wild (♀) × wild (♂)	3.48	66.2	321.3	1.70	0.81	11.3	75.2

this problem was found by the use of crossbreds between strains. A search of the literature revealed six serious studies carried out in different salmonid species in which crossbreds between strains of the same species were compared with one or both of their parental strains. These comparisons were carried out in natural bodies of water, and the traits noted include survival, weight, and thence return. The results of these studies are here considered jointly for the first time in an attempt to project general conclusions. In four of these investigations, involving either cutthroat trout (*Salmo clarki*) or brook trout (*Salvelinus fontinalis*), crossbreds between wild × domestic strains were tested. In a study involving pink salmon, the crossbred was between two wild strains. In these five studies the crossbreds showed a higher return as a result of better survival, faster growth, or both. In a study involving steelhead trout (*S. gairdneri*), the crossbred did not exhibit any advantage over the parental strains. This may be due to a lack of effective genetic differentiation between the parental groups.

Heterosis of return may occur when the crossbred is superior in either survival or growth and equal to one of the parental strains in the other trait. Heterosis may also occur when the crossbred is intermediate in both traits. Even when harvested yield of crossbreds does not exceed that of the wild strain, production costs may be reduced by using domestic spawners of one sex (presumably females) in hatcheries.

Summary of Six Case Studies

1. Cutthroat trout (Donaldson et al. 1957)

Reciprocal crossbreds between a domestic and wild strain of coastal cutthroat trout were compared with their parental strains. The domestic strain had been produced at the School of Fisheries, University of Washington, by 20 yr of selection for season of spawning, rapid growth, early sexual maturity, increased fecundity, disease resistance, and efficient utilization of food. The wild strain consisted of the first generation progeny of a sample of cutthroat trout taken from Lake Whatcom, Washington. The effect of selection on the University of Washington domestic strain is obvious when compared with the Lake Whatcom wild strain, in earlier maturity, larger size of both sexes, average number of eggs at initial spawning, and proportion of mature females. Young-of-the-year samples of four genetic groups (two reciprocal crossbreds and two parental strains) were differentially marked by fin amputation and planted into Echo Lake, Washington (7-ha surface area) in August 1954 and June–July 1955. Records were kept of fish taken by sport anglers on the opening day of the angling season in 1955 and 1956. In 1956, in addition to the 1-yr-old fish planted in 1955, a few 2-yr-old fish from the 1954 planting were also caught by anglers. The results of the 1954 planting (taken from tables 2–9 in Donaldson et al. 1957) are summarized in Table 1. They show that during their first year, growth of the domestic strain was faster than that of the wild strain, with the interstrain crossbreds intermediate. In the second year the wild strain grew faster than the domestic one. The proportion of 1-yr-old crossbreds caught by anglers was much higher than that of either parental strain. For 2-yr-old fish, the proportional catch of the wild strain was similar to that of the crossbreds and higher than that of the domestic strain. The proportional catch out of weight stocked was higher for crossbreds than parental stocks. Only in crossbreds was the total weight of fish taken by anglers greater than that planted. Similar results were obtained from the 1955 planting.

2. Brook trout (Flick and Webster 1976)

A crossbred between a domestic and a wild strain of brook trout was compared with its parental strains and with a further wild strain. The domestic strain, New York, had then been maintained as an inbred line for over 50 yr. The two wild strains, Assinica and Temiscamie, are of Canadian origin (Assinica Lake and Temiscamie River), the fish tested being first generation progenies of wild parents (10–20 individuals in each case). This comparison was part of a population dynamics study including further stocks of brook trout planted into a number of test waters, trap netting, marking and release, as well as angling during 5 or more yr. Only the angling data of Bay Pond is presented here, this being the only water stocked with the four groups of fish mentioned. Bay Pond is a natural basin of 87 ha located in the northern Adirondack Mountains of New York State at an elevation of about 470 m and is relatively infertile.

Young-of-the-year samples of the four genetic groups were stocked into Bay Pond in October 1968, each group being differentially marked by fin clipping. Angling continued during 5 yr, most of the catch occurring in spring. The results, based on angling records considered to be reliable and complete (taken from tables 5 and 6 of Flick and Webster 1976), are presented in Table 2. The largest number of fish in each group was caught in their second year. Fish of the domestic strain were caught by anglers only during the first 3 yr, while wild strain and crossbred fish were caught up to 7 yr. In each year the crossbreds were the largest fish and the domestic strain the smallest. The proportion of crossbreds caught was much higher than that of any other group. Thence the ratio of number caught to number stocked was several times higher for the crossbreds than for either wild or domestic strains. The few fish trapped during the sixth and seventh year were predominantly crossbreds, a few were wild stock fish, and none were domestics. As

TABLE 2. Angling catch of domestic, wild, and domestic × wild strain brook trout stocked into Bay Pond, New York State (after Flick and Webster 1976).

Stock	Domestic (New York)		Domestic × wild (New York × Assinica)		Wild (Assinica)		Wild (Temiscamie)	
No. stocked	2995		3050		3126		1351	
Total weight (kg)	27.17		20.46		13.61		6.08	
Weight/fish (g)	9.1		6.7		4.4		4.5	
	Angling catch							
Age (yr)	No.	Mean wt. (g)	No.	Mean wt. (g)	No.	Mean wt. (g)	No.	Mean wt. (g)
1	2	77	7	136			2	122
2	58	349	242	572	31	354	30	367
3	4	422	38	803	8	603	4	626
4			13	826	12	826	1	635
5			26	844	8	640	5	644
Tot. no.	64		326		59		42	
Tot. wt. (kg)		22.1		202.6[a]		30.8		17.6
No. caught/ no. stocked (%)	2.1		10.7		1.9		3.1	
Weight caught/ weight stocked		0.81		9.90		2.27		2.90
Age (yr)	No. of older fish sampled							
6	0		25		3		4	
7	0		6		0		1	

[a]Given as 204.3 in Flick and Webster (1976).

a result of the larger proportion of crossbred fish caught and their higher mean weights, the ratio of total weight caught to weight stocked was about 10 for the crossbreds, between 2 and 3 for the wild strains, and less than 1 for the domestic strain.

3. Brook trout (Webster and Flick 1981)

Crossbreds between wild and domestic strains were compared with parental strain(s) during their first summer. The wild strains used were from Long Pond Outlet (LPO) and Honnedaga Lake (Honn) in the Adirondack Mountains as well as the two Canadian strains mentioned. Domestic strains were either the New York strain previously described or Cortland, which has also been propagated in captivity for over 50 yr. The study was carried out between 1962 and 1979 by yearly stocking of different groups into Laramie Pond (0.19 ha), situated in the same area as Bay Pond. Fingerlings of 2–5 g were stocked mainly during the second half of June of each year and the pond drained 80–150 d later. Only those cases in which wild × domestic crossbreds and at least one other group were stocked are reported here. The results of four comparisons (taken from table 1 of Webster and Flick 1981) are summarized in Table 3. These include two comparisons between crossbreds and both parental strains (1963 and 1978 year classes) and a further two comparisons involving crossbreds and their wild strain parents only (1975 and 1979 year classes).

The interstrain crossbreds showed the highest survival (except Honnedaga wild strain of the 1963 year class), while that of the domestic strains was the lowest. The mean survival of crossbreds exceeded that of wild and domestic strains by 30 and 65%, respectively. Wild strains showed the slowest growth (during this, their first year) in all cases, possibly due to being stocked at the lowest weight. The ratio of weight recovered to weight stocked was highest for the crossbreds (again with the exception of the Honnedaga strain in 1963), exceeding that of wild and domestic strains by 18 and 81%, respectively.

4. Brook trout (Fraser 1981)

This study included two wild × domestic crossbreds, a wild × wild crossbred, and the purebred parental strains. The wild strains were first generation progenies of fish taken from Lake Nippigon (Nipp) and Dickson Lake (Dick), Ontario. The domestic strain had been domesticated at a hatchery in Ontario for over 20 generations and previously in Pennsylvania with "one infusion of genes from a wild strain of brook trout." Fish of this strain are routinely stocked into Ontario waters, but with unsatisfactory results due to low survival.

Young-of-the-year samples of fingerlings of two or more genetic groups were stocked in September to early October into nine Precambrian Shield lakes in Algonquin Park, Ontario, in the years 1973–77. Fish of different groups were differentially fin clipped before stocking. These study lakes are relatively infertile and range in area between 9 and 27 ha and in maximum depth between 7 and 36 m. Intensive gill netting was carried out annually in all nine lakes and three of them were also fished by anglers during 1974–80. The results (taken from tables 1–4 of Fraser 1981) are summarized in Table 4. The proportional recovery of wild × domestic crossbreds was higher than that of the domestic strain. Recovery of the wild strains was also higher than that of the domestic strain except in Oram Lake. Growth of the domestic strain was slower than that of the wild × domestic crossbred or the wild strains in each

TABLE 3. Performance of domestic, wild, and wild × domestic strain brook trout stocked into Laramie Pond, New York State (after Webster and Flick 1981). LPO = Long Pond Outlet; R/S = total weight recovered/total weight stocked.

Year (days)	Strain			No. of fish		Mean weight/fish (g)		
	Domestic	Wild × domestic	Wild	Stocked	Survival (%)	Stocked	Recovered	R/S
	Cortland			500	39.8	5.5	16.4	1.18
		LPO × Cortland		250	62.0	4.4	15.5	2.21
1963		Honnedaga × Cortland		250	65.6	3.6	15.8	2.85
(115)			LPO	250	52.4	2.2	11.4	2.76
			Honnedaga	250	66.0	2.6	11.3	2.91
1975		Temiscamie × domestic[a]		295	66.1	3.3	10.7	2.17
(79)			Temiscamie	147	55.8	2.1	7.2	1.90
	Domestic[a]			250	44.4	3.0	22.3	3.25
		Assinica × domestic[a]		250	68.8	2.5	18.1	4.95
1978		Temiscamie × domestic[a]		250	74.8	3.2	18.6	4.41
(93)			Assinica	250	50.0	2.3	12.2	2.68
			Temiscamie	250	52.0	2.3	11.4	2.60
		Assinica × domestic[a]		300	62.0	4.2	17.3	2.55
1979		Temiscamie × domestic[a]		300	77.0	4.3	15.4	2.78
(79)			Assinica	300	36.0	2.9	10.5	1.28
			Temiscamie	300	57.0	2.0	12.7	3.62
Total	Domestic			750	41.3	4.3	19.4	1.63
or		Wild × domestic		1895	68.1	3.6	15.9	2.95
mean			Wild	1747	52.2	2.3	10.9	2.49

[a]Not clear whether Cortland or New York.

lake, except Oram. Most of the recovery of domestic fish took place within a year of stocking, whereas that of the other groups was spread over 3–5 yr. The figures given for weight of recovered fish (in Table 4) are somewhat academic and were obtained by back-computation (dividing the total weight recovered by the total number recovered). They represent the weighted means of fish during several years of recovery. Mean weight and growth of the crossbreds and wild strains was about 1.5 times higher than that of the domestic strain in all cases except Oram Lake, in spite of the invariably higher stocking weight of the domestic fish. The mean ratio of weight recovered to weight stocked was over 7 for the Nipp × Dom crossbred, the Dick wild strain, and the Dick × Nipp crossbred, but below 3 for the Dick × Dom crossbred and unity or below for the domestic strain.

5. Steelhead trout (Reisenbichler and McIntyre 1977)

Steelhead trout from wild and hatchery parents and their crossbred were compared. The source of the parent fish was the Deschutes River (a tributary of the Columbia River), Oregon. Spawners were captured from the river in a trap during their upstream migration. Hatchery fish were first generation progenies of wild fish, reared in a hatchery for about 1 yr and then released into the river after fin clipping for identification. The hatchery fish tested were then no more than two generations removed from wild parents. Gametes were taken from these fish and stored at 4°C until a sample of liver tissue of each parent had been analyzed electrophoretically to determine the lactate dehydrogenase-4 genotype. The eggs were then fertilized in a scheme enabling electrophoretic identification of each mating, e.g. for the eggs stocked into Potlid Creek, the hatchery × hatchery mating (HH) was marked B′B′, the hatchery × wild mating (HW) by BB, and the wild × wild (WW) by B′B (see table 1 in Reisenbichler and McIntyre 1977). Counted samples of eyed eggs from each mating were placed in Vibert boxes in screened study sections of 0.8–1.6 km in three creeks (Potlid, Dutchman, and Trout) in February and March 1975. After fry emergence, dead embryos were counted in each box to determine embryo survival. Counted samples of unfed swim-up fry were stocked into a study section of Opal Creek and into a hatchery pond. Samples of juvenile fish were captured by electrofishing on two, three, or four occasions in different creeks and once in the hatchery pond.

The results (taken from tables 2 and 4 of Reisenbichler and McIntyre 1977) are shown in Table 5. Embryo survival was highest for the wild fish in all three creeks and lowest for the hatchery fish in two of them. Similarly, the proportion of juvenile fish caught, out of the total number of eggs, was highest for the wild fish in two creeks and lowest for the hatchery fish. The mean length of fish of each of the three groups was rather similar in each of the four creeks. In the hatchery pond, however, the hatchery fish were the largest and showed the highest proportion of capture.

The study shows a genotype–environment interaction, favoring a hatchery environment for the hatchery fish and a natural environment for the wild fish. Heterosis of crossbreds was not demonstrated. This may be due to the wild and hatchery fish being of the same stock, the Deschutes River. Use of a nonendemic stock for crossbreeding with the indigenous population might have produced different results.

6. Pink salmon (Bams 1976)

The possibility of rehabilitating an almost depleted run of pink salmon was investigated by comparing the performance of a donor stock with that of a crossbred between donor stock females and local males. The low number of ripe females in a depleted system limits fry production, whereas a low number of males may fertilize a large number of eggs from donor

TABLE 4. Performance of domestic, wild, wild × domestic, and wild × wild strain brook trout stocked into nine lakes in Algonquin Park, Ontario (after Fraser 1981). Dom = Hill's Lake Hatchery strain of domestic brook trout; Nipp = Lake Nippigon wild strain; Dick = Dickson Lake wild strain; R/S = total weight recovered/total weight stocked.

Lake	Area (ha) (max. depth (m))	Stocks	No. of fish/ha		Mean weight/fish (g)		R/S
			Stocked	% recovery	Stocked	Recovered	
Little	9.3	Dom	75	7.4	14.4	408.6	2.1
Mykiss	(6.7)	Nipp × Dom	77	4.7	6.4	535.5	12.3
Shallnot	9.3	Dom	75	2.2	14.4	392.7	0.6
	(7.3)	Nipp × Dom	75	9.9	6.4	588.2	9.1
Chipmonk	27.1	Dom	59	3.0	14.4	288.0	0.6
	(16.8)	Nipp × Dom	62	6.9	6.4	473.1	5.1
Rumley	18.1	Dom	48	1.1	14.4	523.4	0.4
	(10.1)	Nipp × Dom	50	3.3	6.4	601.4	3.1
Mean		Dom	64	3.4	14.4	403.2	1.0
		Nipp × Dom	66	8.7	6.4	549.6	7.4
Little	8.9	Dom	79	4.8	14.4	150.1	0.5
Minnow	(14.3)	Dick × Dom	75	11.3	10.6	196.9	2.1
Presto	15.5	Dom	79	1.3	14.4	222.0	0.2
	(35.7)	Dick × Dom	77	1.6	6.7	503.3	1.2
Oram	27.1	Dom	76	7.4	12.2	264.0	1.6
	(18.3)	Dick × Dom	65	8.6	6.3	227.3	3.1
		Nipp	63	3.4	6.8	220.2	1.1
Mean		Dom	78	4.5	13.7	212.0	0.8
		Dick × Dom	72	7.2	7.9	309.2	2.1
Major	26.3	Dom	78	8.9	11.9	93.6	0.7
	(14.6)	Dick	80	10.4	3.3	130.1	4.1
Mykiss	23.5	Dom	67	4.0	12.5	249.6	0.8
	(11.3)	Dick	54	13.2	5.7	427.6	9.9
		Dick × Nipp	46	9.9	5.4	496.8	9.1
Mean		Dom	73	6.5	12.2	171.6	0.8
		Dick	67	11.8	4.5	278.9	7.0

TABLE 5. Performance of steelhead trout from Deschutes River hatchery-raised and wild parents and their crossbred stocked into four creeks flowing into Deschutes River, Oregon (after Reisenbichler and McIntyre 1977). H = progeny of fish captured in Deschutes River and reared in Oregon Department of Fish and Wildlife Hatchery; W = fish captured in Deschutes River.

Stage stocked	Location	No. stocked per group	Survival of embryos (%)			Proportion of fish captured (%)			Mean length of final sample (mm)		
			HH	HW	WW	HH	HW	WW	HH	HW	WW
Eyed eggs	Potlid Creek	9000	89	83	93	2.7	2.7	2.8	62	65	63
	Dutchman Creek	9000	70	72	78	3.9	4.3	4.1	70	68	70
	Trout Creek	6000	75	84	86	2.1	2.8	4.3	54	52	52
Swim-up fry	Opal Creek	7500				5.5	5.6	7.2	63	65	63
Mean			78.4	79.5	86.1	3.6	3.9	4.5	62.3	62.5	62.0
Swim-up fry	Hatchery Pond	6000				3.3	2.6	2.4	60	56	56

females.

Fish for spawning were seined from two rivers in British Columbia. The local males were seined from Tsolum River. Donor females and males were collected from Kakweiken River, which had large yearly runs of pink salmon. Eggs of Kakweiken females were fertilized with milt taken from either Kakweiken or Tsolum males in September to October 1972. Incubation was carried out in vertical stock incubators and then gravel incubators, and survival to eyed eggs and fry emergence was determined. The emergent fry were marked by fin clipping and released into a creek entering the Tsolum River. In the subsequent year, adult returns were determined, first by inspec-

tion of the commercial catch in coastal waters at two fish processing plants. After passage through the inshore waters, returning adults were collected in the river systems. The results of these comparisons (taken from tables 1, 2, and 4 of Bams 1976) are summarized in Table 6.

Crossbred and donor purebreds differed little in survival to eyed eggs or fry emergence. The two groups were represented in the commercial catch of returning adults in approximately the same ratio as that of their number released. However, the number of adults recovered in the river system was much higher for crossbreds than donor purebreds (236 versus 45 fish). Most of these fish were recovered in the Tsolum River, at different distances from the point of release. For the crossbreds there was a clear correlation between number of fish and proximity to the point of release, but this was not the case for the donor purebreds. Eight crossbreds, but no purebreds, were also found in a creek only indirectly connected with the Tsolum River. Additional seinings in two other rivers, including the Kaweiken River, failed to collect fish of either group.

TABLE 6. Performance of purebred donor and donor × natal strain pink salmon released into Tsolum River, British Columbia (after Bams 1976). Donor = Kakweiken River strain; Natal = Tsolum River strain.

Genetic group	Purebred (donor × donor)	Crossbred (donor × natal)
Survival (%)		
Green to eyed eggs	72.0	84.2
Eyed eggs to fry emergence	96.2	96.3
No. marked and released	109 658	124 792
No. recovered		
Offshore	205	247
Rivers		
Tsolum River	10	104
H. Q. Weir		
Section A	13	70
Section B	10	35
Section C	6	17
Section D	6	2
Morrison Creek	0	8
Kakweiken River	0	0
Oyster River	0	0
Total rivers	45	236
Grand total	250	483

Discussion

The declines in many natural fisheries are clearly a direct result of overfishing and pollution. I have attempted to show that these causes also brought about genetic changes in the fish populations involved, which, unless counteracted, make recoveries unlikely. This may possibly be accomplished in restocking programs through choice of the genotypes stocked. The data reviewed in this article demonstrate heterosis of first generation interstrain crossbreds in performance in natural waters. Thence, stocking F1 crossbreds is expected to give a higher return than stocking purebred strains, when the fish stocked are not expected to reproduce in the natural environment. Yearly stocking of large numbers of fry or fingerlings is required for this type of stocking program to be effective. Use of F1 crossbreds may be particularly effective when catchable-sized fish are stocked. This is an established practice with rainbow trout in California (Rawstron 1977) and recommended for brook trout in Maine (Havey and Locke 1980). Most of the fish are taken by anglers after a short residence in the stocked waters. Often, less than half the number of stocked fish are recovered and the weight return may be less than the weight planted. The cost of fish taken by anglers varied in different studies. For rainbow trout in Californian lakes, brook trout in a lake in Maine, and walleye in a reservoir in Virginia, costs were estimated as \$0.99−3.28/kg fish, \$3.91−4.69/fish, and \$27.35/fish taken by anglers, respectively (Rawstron 1972, 1973, 1977; Havey and Locke 1980; Murphy et al. 1983). Possibly, by stocking F1 rather than purebreds, the cost could be reduced considerably.

When the aim of the stocking program is to enhance a self-perpetuating population, stocking domesticated strain spawners (of one sex) may result in F1 production through their interbreeding with the resident population. The resident fish will also spawn between themselves. Backcross and F2 generations may be produced after the F1 crossbreds mature. This situation has been described by Moav et al. (1978) and consists of genetically upgrading the resident population. A similar situation is expected in lakes not inhabited by a resident population of wild fish, stocked with wild spawners of one sex and domestic ones of the other, or crossbred fingerlings.

No empirical evidence is available for the superiority of these F2, backcross, etc., generations over purebred resident stocks. Presumably this depends on the genetic constitution of the resident and donor stocks. One may expect an immediate improvement resulting from interbreeding between the stocked and resident strains, followed by a decline in subsequent generations. A long-term improvement is likely to require periodic stocking of spawners of one sex of the donor stock until a stable population has been established. Two recent publications deal with the genetic management of wild fish populations.

Krueger et al. (1981) assumed that the genetic causes for the depletion of natural fisheries is the lack of sufficient genetic variation. They proposed two strategies for increasing genetic variation of fishes in rehabilitation programs: (1) "Making separate collections of fish from each of several genetically different populations, performing all possible crosses between the different sources, and then stocking the progeny." "By maximizing the possible genetic combinations, it is hoped that by chance some will be fit for the new environment and will, therefore, disproportionately contribute to the gene pool of subsequent generations." (2) "To sample from populations that are environmentally similar to those being rehabilitated and which may contain preadapted genotypes."

A conceptual fitness model for managing Pacific salmon fisheries, developed by Kapuscinski and Lennan (1984), could in principle be applied to other fish populations. The model is aimed at "maintaining the variance of fitness at a level allowing the stock to perpetuate itself in face of fishing and natural mortality." It relates variance of fitness to number of spawners, age structure of the population, and rate of immigration. "The prevelant belief that native fish are always genetically superior to transplanted by long evolved specific gene complexes, highly adapted to their locality" is doubted by Kapuscinski and Lennan (1984).

A single introduction of wild stocks is thus recommended by

Krueger et al. (1981). Kapuscinski and Lennan (1984) do not differentiate between wild and hatchery stocks. Rates of immigration required by their model imply repeated stockings, as I have suggested here. Neither study specifies methods of application, i.e. evaluation of stocks, monitoring the results of stocking programs, and choice of suitable locations for testing.

Choice of Stocks and Crossbreds

Testing programs could be initiated with crossbreds between domestic females and wild males of a strain native to the water to be restocked. Use of domestic stocks as female parent reduces cost of production in the hatchery, while endemic males make the comparison with the native stock, used as control, more meaningful. This does not preclude testing other genetic combinations at a later stage, possibly including domestic × domestic or wild × wild crossbreds.

Monitoring the Results of Stocking Programs

The most obvious monitoring method consists of comparing the yield characteristics of the different groups stocked. This should be carried out over a number of years and in adjacent areas as well as the one actually stocked. Genetic monitoring is also required to determine gene segregations in generations beyond the one stocked. Use of genetic marking with morphological mutations is limited by the small number of available mutations (e.g. gold in rainbow trout). Most are simple Mendelian alleles, which makes the heterozygotes indistinguishable from one of the homozygotes. Genetic monitoring is, therefore, best carried out with the help of electrophoretic markers. These are codominant as a rule and their number is large. The use of electrophoretic markers as genetic monitors in stocking programs has been described by Moav et al. (1978) and others. It consists of marking the introduced stocks with electrophoretic alleles at a number of loci, distinct from those present in indigenous stocks. When the stocked fish do not possess distinct electrophoretic alleles, it may still be possible to monitor and evaluate the effects of stocking from shifts in allelic frequencies (Murphy et al. 1983). Monitoring should be carried out in adjacent ecosystems as well as the one stocked in order to evaluate the possible results of migration to neighboring areas.

Scale and Locations for Testing Stocking Programs

In order to minimize possible deleterious effects of stocking programs, they could be initiated in relatively small lakes or streams, isolated from other bodies of water. If damage to the ecosystem appears to occur, the program should be discontinued in the hope that the negative results will dissipate in a relatively short time. If the stocking program appears ineffective but not detrimental, it might be repeated with different stocks or in a different body of water. If, however, the results are positive, as anticipated, stocking programs of this type could be augmented on an increasing scale and in larger and less isolated bodies of water. In this case it seems likely that the effectiveness of stocking programs will be increased, that there will be ample returns for the funds invested, and that additional employment possibilities will be created for fisheries scientists.

Acknowledgments

My thanks to my friend, mentor, and colleague, Professor Rom Moav, who suggested the idea of genetic improvement of wild fish populations by the use of crossbreds. We discussed a previous draft of this paper before his untimely death in 1984. He made a number of suggestions which I adopted.

NOTE ADDED IN PRESS: After writing this article, I came across a paper, previously overlooked, dealing with brook trout of wild and domestic strains and a domestic × wild crossbred, stocked into five streams in Wisconsin (Mason et al. 1967). Recovery per unit weight stocked is somewhat difficult to assess, as only the length of fish recovered, and not their weight, was noted. Differences between these groups, in survival and recovery, are smaller than those found in the three brook trout tests described. Mean survival of the crossbred was slightly higher than that of the other groups. Its mean relative recovery was practically equal to that of the wild strain. The domestic strain, routinely released into Wisconsin streams, showed the lowest estimates in both traits.

Reference: Mason, J. W., O. M. Brynildson, and P. E. Degurse. 1967. Comparative survival of wild and domestic strains of brook trout in streams. Trans. Am. Fish. Soc. 96: 313–319.

References

ANTHONY, D. D., AND C. R. JORGENSEN. 1977. Factors in the declining contribution of walleye (*Stizostedion vitreum vitreum*) to the fisheries of Lake Nipissing, Ontario, 1960–76. J. Fish. Res. Board Can. 34: 1703–1709.

BAMS, R. A. 1976. Survival and propensity for homing as affected by presence or absence of locally adapted paternal genes in two transplanted populations of pink salmon (*Oncorhynchus gorbuscha*). J. Fish. Res. Board Can. 33: 2716–2725.

BERST, A. H., AND G. R. SPANGLER. 1972. Lake Huron: effects of exploitation, introductions, and eutrophication on the salmonid community. J. Fish. Res. Board Can. 29: 877–887.

BRUHN, D. S., AND J. T. BOWEN. 1973. Selection of rainbow trout brood stock, 1968. Prog. Fish-Cult. 35: 119–120.

CHRISTIE, W. J. 1972. Lake Ontario: effects of exploitation, introduction, and eutrophication on salmonid communities. J. Fish. Res. Board Can. 29: 913–929.

COLBY, P. J., G. R. SPANGLER, D. A. HURLEY, AND A. M. MCCOMBIE. 1972. Effects of eutrophication on salmonid communities in eutrophic lakes. J. Fish. Res. Board Can. 29: 975–983.

CORDONE, A. J., AND S. J. NICOLA. 1970. Harvest of four strains of rainbow trout, *Salmo gairdneri*, from Beardesley Reservoir, California. Calif. Fish Game 56: 271–287.

DAVIDOFF, E. B., R. W. RYBICKI, AND K. H. DOAN. 1973. Changes in the population of lake whitefish (*Coregonus clupeaformis*) in Lake Winnipeg from 1944 to 1969. J. Fish. Res. Board Can. 30: 1667–1682.

DONALDSON, L. R., D. P. HANSLER, AND T. H. BUCKRIDE. 1957. Interracial hybridization of cutthroat trout, *Salmo clarkii*, and its use in fisheries management. Trans. Am. Fish. Soc. 86: 351–360.

DONALDSON, L. R., AND D. MENASVETA. 1961. Selective breeding of chinook salmon. Trans. Am. Fish. Soc. 90: 160–164.

EMBODY, E. E., AND C. D. HAYFORD. 1925. The advantage of rearing brook trout fingerlings from selected breeders. Trans. Am. Fish. Soc. 55: 135–148.

ESHENRODER, R. L. 1977. Effects of intensified fishing changes and spring water temperatures on yellow perch, *Perca flavescens*, in Saginaw Bay. J. Fish. Res. Board Can. 34: 1830–1838.

FALCONER, D. S. 1960. Introduction to quantitative genetics. Oliver and Boyd, Edinburgh. 365 p.

FLICK, W. A., AND D. A. WEBSTER. 1964. Comparative first year survival and production in wild and domestic strains of brook trout, *Salvelinus fontinalis*. Trans. Am. Fish. Soc. 93: 58–69.

1976. Production of wild, domestic, and interstrain hybrids of brook trout (*Salvelinus fontinalis*) in natural ponds. J. Fish. Res. Board Can. 33: 1525–1539.

FRASER, J. M. 1981. Comparative survival and growth of planted wild, hybrid, and domestic strains of brook trout (*Salvelinus fontinalis*) in Ontario lakes. Can. J. Fish. Aquat. Sci. 38: 1672–1684.

GWAHABE, J. J. 1973. Effects of fishing on the *Tilapia nilotica* (Linnee 1757) population in Lake George, Uganda over the past 20 years. E. Afr. Wildl. J. 11: 317–328.

HANDFORD, P., G. BELL, AND T. REIMCHER. 1977. A gillnet fishery considered as an experiment in artificial selection. J. Fish. Res. Board Can. 34: 954–961.

HAVEY, K. A., AND D. O. LOCKE. 1980. Rapid exploitation of hatchery-reared brook trout by ice fishermen in a Maine lake. Trans. Am. Fish. Soc. 109: 282–286.

HAYFORD, C. O., AND C. E. EMBODY. 1930. Further progress in selective breeding of brook trout at New Jersey State Hatchery. Trans. Am. Fish. Soc. 60: 109–118.

KAPUSCINSKI, A., AND J. E. LENNAN. 1984. Applications of a conceptual fitness model for managing Pacific salmon fisheries. Aquaculture 43: 135–146.

KELEHER, J. J. 1972. Great Slave Lake: effects of exploitation on the salmonid community. J. Fish. Res. Board Can. 29: 741–753.

KENYON, R. 1978. Growth changes in a population of whitefish in Lake Erie. N.Y. Fish Game J. 25: 129–139.

KRUEGER, C. C., A. J. GHARRET, T. R. DEHRING, AND F. A. ALLENDORF. 1981. Genetic aspects of fisheries rehabilitation programs. Can. J. Fish. Aquat. Sci. 38: 1877–1881.

LARKIN, P. A. 1979. Maybe you can't get there from here: a foreshortened history of research in relation to management of Pacific salmon. J. Fish. Res. Board Can. 36: 98–106.

LAURENT, P. J. 1972. Lac Leman: effects of exploitation, eutrophication, and introductions on the salmonid community. J. Fish. Res. Board Can. 29: 867–875.

LAWRIE, A. H., AND J. F. RAHRER. 1972. Lake Superior: effects of exploitation and introduction on the salmonid community. J. Fish. Res. Board Can. 29: 765–776.

LEWIS, R. C. 1944. Selective breeding of rainbow trout at Hot Creek hatchery. Calif. Fish Game 30: 95–97.

LOFTUS, K. H. 1976. Science for Canada's fisheries rehabilitation needs. J. Fish. Res. Board Can. 33: 1823–1857.

MILLENBACH, C. 1950. Rainbow brood stock selection and observation in its application to fisheries management. Prog. Fish-Cult. 12: 151–152.

MILLER, R. B. 1952. Survival of hatchery-reared cutthroat trout in an Alberta stream. Trans. Am. Fish. Soc. 81: 35–42.

1958. The role of competition in the mortality of hatchery trout. J. Fish. Res. Board Can. 15: 27–45.

MOAV, R., T. BRODY, AND G. HULATA. 1978. Genetic improvement of wild fish populations. Science (Wash., DC) 201: 1090–1094.

MURPHY, B. R., L. A. NIELSEN, AND B. J. TURNER. 1983. Use of genetic tags to evaluate stocking success for reservoir walleyes. Trans. Am. Fish. Soc. 112: 457–463.

RAWSTRON, R. R. 1972. Harvest, survival and cost of two domestic strains of tagged rainbow trout in Lake Berryessa, California. Calif. Fish Game 58: 44–49.

1973. Harvest, mortality and cost of three domestic strains of tagged rainbow trout stocked into large California impoundments. Calif. Fish Game 59: 245–265.

1977. Effect of reduced bag limit and later planting date on the mortality, survival, cost and yield of three domestic strains of rainbow trout at Lake Berryessa and Merle Collins Reservoir, 1971–1974. Calif. Fish Game 63: 219–227.

REISENBICHLER, R. R., AND J. D. MCINTYRE. 1977. Genetic differences in growth and survival of juvenile hatchery and wild steelhead trout, *Salmo gairdneri*. J. Fish. Res. Board Can. 34: 123–128.

RICKER, W. E. 1981. Changes in the average size and average age of Pacific salmon. Can. J. Fish. Aquat. Sci. 38: 1635–1656.

ROTH, H., AND W. GEIGER. 1972. Brienzersee, Thunersee, and Bielersee: effects of exploitation and eutrophication on the salmonid communities. J. Fish. Res. Board Can. 29: 755–764.

SMITH, S. B. 1961. Selectivity and hybridization in management of fish stocks. Can. Fish Cult. 29: 25–30.

TONEY, D., AND J. T. BOWEN. 1968. Selection of rainbow trout brood stock. Prog. Fish-Cult. 30: 120.

WEBSTER, D. A., AND A. F. FLICK. 1981. Performance of indigenous, exotic, and hybrid strains of brook trout (*Salvelinus fontinalis*) in waters of the Adirondack Mountains, New York. Can. J. Fish. Aquat. Sci. 38: 1701–1707.

WELLS, L., AND A. L. MCLAIN. 1972. Lake Michigan: effects of exploitation, introduction, and eutrophication on the salmonid community. J. Fish. Res. Board Can. 29: 889–898.

BOOK REVIEWS / COMPTES RENDUS

Seafood toxins. *edited by Edward P. Ragelis. American Chemical Society Symposium Series 262. 1984. 460 p. $79.95 (Canada and U.S.), $95.95 (other countries). ISBN 0-8412-0863-8.*

This book is another example of the excellent ACS Symposia series which might have been entitled "Everything you wanted to know about Marine Toxins but were afraid to ask." The book contains contributions (each in the form of a research paper) from experts throughout the world and covers the biology, taxonomy, ecology, and chemistry of marine and some freshwater toxins. Because of the nature of the book, there is some repetition among the individual papers and the book appears a little disjointed at times as the reader is asked to switch from topic to topic.

The book is divided into six segments: an introductory overview and segments entitled Shellfish Toxins, Ciguatera, Tetrodotoxin, Toxins from Red Tide and Cyanobacteria, and Scombroid Fish Poisoning. Generally speaking it is obvious to which segment each contribution belongs, but it is not clear why the excellent papers by Ragelis and Doorenbos on ciguatera toxins are included in the Overview rather than the Ciguatera segment. The same can be said for the paper by Yentsch and that by Nevé and Reichdardt which deal with Paralytic Shellfish Poisons (PSP) toxins.

Studies on marine toxins are concerned with five main points: what are they, where do they come from, how are they produced, how do they work, and how can they be detected. All of these points are considered in varying degrees in each segment. Greatest space is devoted to PSP's which are the most studied and best understood toxins. The next most covered group are the ciguatera toxins, then red tide and cyanobacterial toxins, three papers dealing with scombroid fish poisoning, and surprisingly only two contributions dealing with tetrodotoxin. This is disappointing because the tetrodotoxin story is an interesting one and provided chemists with several severe challenges in the 1960's.

Nevertheless the reader is treated to some excellent contributions including Halstead's detailed article in the Overview which describes the many other cases of marine intoxications which may or may not be related to the more well known toxins. Schantz's chapter is a beautiful pocket autobiography of his pioneering work on PSP toxins, and the excellent chapter by Shimizu and his collaborators is an up-to-the-minute account of their attempts to determine the biogenesis of these unusual metabolites. The section on ciguatera toxins is well dealt with, in large part due to several interesting contributions from the Southern Illinois University group, and a thorough account by Lewis of the increasing incidence of intoxication and its implication for small-scale commercial fisheries in the Pacific. The chapter by Mosher and Fuhrman, concerning the origin of tetrodotoxin — a product of a symbiotic organism? — is particularly thought provoking, especially in light of the very recent demonstration that the surugatoxins, of the ivory shell *Babylonia japonica*, have a microbial origin. The brevetoxins are adequately dealt with in a single paper which is combined with four papers dealing with freshwater and marine cyanobacterial toxins. The book finishes with three strong papers on scombroid fish poisoning, a worldwide, unpleasant, but usually nonfatal disease arising from ingestion of large amounts of histamine and associated with many varieties of fish.

Although known since antiquity, marine toxins continue to be topical and consistently provide rewarding science and fascinating anecdotes (not antidotes!). This book certainly reflects these characteristics, and is highly recommended.

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Concepts in marine pollution measurements. *Edited by Harris H. White. Maryland Sea Grant College, University of Maryland, College Park, MD. 1984. 743 p. $12.50 U.S. (cloth). ISBN 0-943676-19-5.*

I must admit that, when faced with a nearly two inches thick, hardbound book with anything resembling the word "concepts" in the title, I tend to delay getting into it. "Conceptualizing" about anything leaves me uninterested. The term is used too often to becloud an issue or a point, and all too often it becomes the screen of verbage behind which to hide ignorance.

This was for me the case also with Harris White's edited book *Concepts in Marine Pollution Measurements*. It smacked of "tome-y," and on opening it, it looked "tome-y." It is a thick book, appearing weighty with many tables, figures, and even a three-page Fortran computer program. Also, I had been aware of some of the not so gratifying comments about the workshop that led up to this publication. Until I finally seriously sat down to read it. And was pleasantly surprised. Because it addresses, as well as any edited workshop proceedings can, that most vexing question of environmental science — how can we predict an environmental impact in the field? It does not provide answers — but there are in this book some good people writing some good ideas.

Going back to the beginning, the notion to try to consolidate some of the thinking about the validity of toxicity tests and laboratory studies vis-à-vis field studies, etc., originally arose some years ago within a small circle within NOAA/Washington that concerns itself with environmental impact statements. Not that this was a new concern, because it was not. Virtually every conference over the last 10 or 15 years, detailing some aspect of man-made environmental impact, has devoted at least some part of its program to discussions about credibility of toxicity tests, acute lethal mortality tests, microcosm testing, or simulated field studies. And any gathering of reasonably intelligent environmental scientists has worried and gnawed at this question of what is meaningful evaluation of environmental impact. One such attempt was the

convening in 1982 of a several-day workshop with the ingenuously disarming title "Meaningful Measures of Marine Pollution Effects". Ingenuous and disarming because it implied a clear statement of the problem of environmental impact assessment, and promised the means whereby to do this — once and for all. And that of course is where is the rub. Because the state of environmental science is only just now at the point where we can speak of it as a science, with some defined boundary conditions, and some notion of underlying principles, i.e. our environmental science is a very young discipline, as yet very poorly understood, and with its outlines still very blurred. For example, where in other scientific disciplines there is a body of data and knowledge which can be shaped into theories, in the environmental science discipline even the body of data is sparse, fragmented, heterogeneous of origin or comparability, and all too often of uncertain value. That is no one's fault. That is the way a discipline develops maturity, by expanding on existing little data points and broadening the relationships between them. We, here in the 1980's and shortly into the 1990's, just happen to be in at the beginning of the growing and consolidation process.

This book, and its various contributors, makes one worthwhile contribution which justifies all the effort that went into it — it spells out many of the identifiable problems in making pollution impact measurements. It also goes a long way toward defining the very broad scope of environmental science. But the reader has to go into the text and the individual papers to get at some of this.

The book is essentially an edited proceedings of papers presented at the 1982 workshop. Invited participants, and author–contributors, were from all points of the environmental compass. And they were enjoined by the workshop organizers to, as frankly as possible, criticize the various aspects and methods of pollution measurements. Which encouragement no doubt led to some of the less favorable rumblings that surfaced post-workshop. Few of us like, honestly, to have our work analyzed for "debilitating features."

The product is a series of 35 papers, spread out over eight chapters. Each chapter is prefaced by a chairperson's introduction which serves both to tie together that chapter's papers as well as provide some sense of overview and summation. The chapters form a reasonable progression, beginning with Chapter 1 that deals with the meaning and utility of toxicity testing in environmental pollution assessments. This is followed naturally by a group of papers dealing with laboratory microcosms (Chapter 2), measurements at the level of communities (Chapter 3), bioaccumulation tests (Chapter 4), meaningful chemical measurements in the environment (Chapter 5), anomalies in field studies (Chapter 6), the use of larger scale mesocosms and field enclosures (Chapter 7), and finally field monitoring programs (Chapter 8). The final chapter (Chapter 9) is a summary and closing synthesis of the workshop and the papers, prepared by the organizers.

The participants and author–contributors generally represent an expert section of pollution science with the likes of Woolcott Smith, John Cairns and colleague Arthur Buikema, Saul Saila, Don Boesch, Dick Lee, Bob Huggett, Don Malins and colleagues, Rita Colwell, Roger Green, Candace Oviatt, Alan Mearns and Tom O'Connor, and the Grassles among others. The knowledgeable reader can therefore spot the obvious tenor of some of the papers — from pollution/tissue anomaly coincidences (Malins et al.) to statistical evaluation (Saila, Smith) and design of monitoring strategies (Green, Boesch). Each paper is relatively brief, averaging about 12–15 pages of text plus figures and references. Individual papers are also fairly well focussed, each covering some particular point or feature of pollution measurement adequately, without straying too far off track or off into subtle details of some data set of particular interest to its author. The brevity does tend to make for regrettable terseness (Woolcott Smith's paper on usefulness of diversity and similarity indices in environmental work) and excessive simplicity in some others (relying for example on one or two case histories or examples to support a conclusion).

The theme that runs throughout these proceedings is of course the problem of increasing complexity of organization and parameters as one proceeds from the organism to the population and through the community to the ecosystem. It thus would seem very obvious that a single-species toxicity test has little or no relevance to or predictive value for implying impact at the ecosystem level. But that of course is unfortunately more or less the current state of the art in pollution measuring, and as Cairns and Buikema point out (p. 103), much of the regulatory opinion appears based on the view that simple "water quality criteria, often based on single species tests, are adequate to protect higher levels of biological organization including communities and ecosystems."

So why not measure the higher order effects, at the community or ecosystem level directly? Again the reasons are marvelously simple. One — we know more or less how to do a reasonable valid measurement on a single organism. But two — we are less certain with a group of organisms, and run into overwhelming problems with entire systems. The simple reason is, of course, that we could theoretically reconstruct, quantitatively, a community or ecosystem from its myriad components — one by one, off the biological supply house shelf if you wish. But we cannot reconstruct even a small subset of one of these, qualitatively or functionally, because the processes that drive the system are either poorly understood or not yet defined. Which means that we do not know which parameters to measure at the community or ecosystem level that most accurately reflect the pollution impact at those levels.

Another reason is much more mundane — the financial price tag that goes with even a simple community measurement is so much higher than that of any number of single toxicity tests that the latter invariably are funded in favor of the former.

The eventual answer or solution to the quandary of course is to develop a much better understanding of how an organism fits within its population, and in turn within the community and ecosystem so that measurements made at some of the lower levels of organization can be related to some perturbation at the next higher level. As well, as the workshop summary concludes, no single index can adequately reflect the health or debilitation of a system, be it organism or ecosystem.

Some highlights in *Concepts in Marine Pollution Measurements*? I appreciated the sequence of three papers, and three approaches, on the use of microcosms in environmental testing (Chapter 2). While one may quibble or disagree with specific approaches or methodology, together they demonstrate that a microcosm is not a microcosm is not a microcosm, and that there are definite and even expected shortcomings. Chapter 3 is given over largely to the community theoreticians, but this reviewer's interest was in Jeffries' perception of a biochemical image of a community, a "holistic insight from biochemical correlates" (p. 213). To this reviewer, at least, it seems that biochemical/physiological indices are ultimately closer to the dynamic structure of an ecosystem than are any

number of diversity or similarity indices and substrate and other physical measurements. On the other hand, it can be argued that the numbers of this or that must depend on the biochemical/physiological "well-being."

The seven papers that make up the chapter on bioaccumulation essentially and broadly summarize the state of the art as we know it today. Two important points are made, however, that are worth reemphasizing. Petrocelli in his introduction to the chapter (p. 248) notes that few studies have examined the correlation between body burden (tissue contaminant load) and adverse effect on the organism. The point is significant because all too often a contaminant is viewed as deleterious, based solely on its high tissue concentrations, i.e. high bioaccumulation or bioconcentration potential. Regrettably this erroneous view ignores the potentially greater toxic threat from those more readily degradable xenobiotics which, by virtue of their ready voidance from tissues, show an apparent low bioconcentration potential. Yet the total accumulated amount passing through the organism over time may well be equally as high as that of the less mobile contaminant with the expressed higher tissue burden. Lee also implies this problem in assessing the significance of tissue burdens in the case of highly lipophilic contaminants that become sequestered in lipid-rich storage tissues. The other point, raised by Jenkins and Brown (p. 369), is that of the physiological cost to the organism of depuration and detoxification of its contaminant tissue burden. This cost is in the form of "energy required for the synthesis of detoxification proteins, competition for amino acids or the physical cost of accumulating large quantities of proteins and/or membrane-bound vesicles within a cell." Certainly these processes are competitors in the metabolic energy-flow. These essential processes are all energy-requiring, do not come free, and are on the debit side of the detoxification equation. It is an aspect of pollution that is not often appreciated, or at least infrequently mentioned in the current literature, but that is nonetheless real.

The title of Chapter 6, "Anomalies in Field Specimens," is a bit misleading, implying some appearance of peculiar or unexpected data points (the "outliers") in field data sets — which would have been interesting. In fact, the chapter simply addresses effects of pollutants — shifts in dominance in pelagic microbial populations in pharmacological waste receiving waters, changes in the adenylate energy-charge system in a range of test organisms, toxicity impact on crustacean larvae, and incidence of tumorigenesis and diseases in wild fish populations. In a way, this chapter would have fitted better at the end of the book, after the chapters on mesocosms and field monitoring programs, because it would have been nice to read through all the "methodological" sections first and then read these case histories in the light of all the comments and criticism of the existing methods of measurement.

The subsequent series of papers on the design and use of mesocosms and related field studies forms the most cohesive set in the entire book. Prepared by experts thoroughly familiar with the workings of mesocosms, the series is the best thing in the entire volume, and should be read by all environmental scientists. One warning — the authors are all adamant and enthusiastic mesocosm-study advocates, and that soon becomes very apparent. To be fair, the use of mesocosms is now generally viewed as the essential and necessary bridge between the single-species test and laboratory experimentation and the field program. And as Oviatt points out in her nice flat-out opening sentence (p. 539): "mesocosms and field enclosures enable us to experiment with whole ecosystems."

Don Boesch's introduction to the chapter on field monitoring programs can stand as an example of how an introduction should be written. Regrettably, Boesch did not contribute a further paper to the proceedings. The gap is filled nicely, however, by Green, Smayda, and the other session-contributors.

Overall assessment? The book is a good contribution to environmental science, and that tricky aspect — measurement of pollutants and pollutant-related perturbations. In going back, again, through the papers three points stood out. One — that attempts to extrapolate from laboratory bench measurements to the field go countercurrent to an overwhelming increase in complexity. As Mount (1979) has pointed out, the probability of predicting community effects with laboratory data may be useful if the effects to be measured are themselves gross. But the success will be negligible or zero as the sought-after effects are refined. Two — the need for agreement, among ecologists, on the parameters that provide the most meaningful information (e.g. Cairns and Buikema, p. 85). Three — laboratory tests and experimental verification studies can be short term. The converse is that meaningful field programs, because of the concomitant increased complexity of organization and function, must be long term. This is shared by several of the participant–authors (e.g. Malins, Smayda, Oviatt).

Obvious gaps? Of course there are always obvious and not so obvious gaps, especially in hindsight. But Rome wasn't built in a day. So let us do the best we can, and proceed with trying to solve the problem of pollution in our environment.

Recommendation? *Concepts in Marine Pollution Measurements* is worth purchasing, and it should be required reading for every environmental scientist, and definitely for the so-called regulators. It shows that there is a very serious and scientifically rigorous side to what some critics may perceive as endless testing for LC50's.

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